

A New Genus of Freshwater Triclad
from Tasmania, with Reviews of
the Related Genera *Cura* and *Neppia*
(Turbellaria, Tricladida)

Ian R. Ball





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(Turbellaria, Tricladida)

This paper is dedicated to Dr. Roman Kenk on the occasion of his
76th birthday.

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A New Genus of Freshwater Triclad from Tasmania, with Reviews of the Related Genera *Cura* and *Neppia* (Turbellaria, Tricladida)

Abstract

A new genus of freshwater planarian, *Romankenkius* gen. nov., is erected to contain two new species, *R. kenki* sp. nov. and *R. pedderensis* sp. nov., described from Tasmania. A critical review of the related genera *Cura* Strand and *Neppia* Ball is provided, and the concepts of these genera are revised. The systematic and biogeographical implications of the new data and opinions are discussed.

Introduction

In the present paper one new genus and two new species of freshwater planarians are described from Tasmania. On most currently accepted classifications of the Paludicola these species would have to be assigned to the genus *Cura* Strand because the testes are restricted to the prepharyngeal region. However, the two new species are not most closely related to the type species of this genus, *Cura foremanii* (Girard), and so a new genus has been erected to contain them. Detailed comparisons with similar species proved necessary, and so I have also taken the opportunity to review all the Dugesiidae which possess testes of restricted distribution. The background to this review is best presented by reviewing the history of the genus *Cura*.

In its broad sense (e.g., Kawakatsu, 1969a) *Cura* is one of the most widely distributed of the freshwater triclads. It is also an old and primitive genus and therefore is of considerable phylogenetic and biogeographical importance (Ball, 1974a). Despite this, the genus, in common with most other genera of aquatic triclads, has never been monographed, and our knowledge is confined mainly to species descriptions from various regions of the world. All too frequently these descriptions contain only the minimum of diagnostic data, and thus they are of limited phylogenetic and biogeographical value.

Cura Strand, 1942, is a replacement name for *Curtisia* von Graff, 1916, which, although preoccupied, was established for a single North American species, *Planaria sirp.plicissima*, i.e. the *Planaria simplissima* of Curtis (1900). These latter names are themselves invalid because priority must be given to the senior synonym *Dugesia foremanii* Girard, 1852 (Stringer, 1918).

The first clear definition of the genus was provided by Kenk (1930), and he also assigned *Planaria patagonica* Borelli, 1901, and *P. michaelsoni* Böhmig, 1902, to the genus. Hyman's (1931) reference to these as European species is erroneous; they are endemic to southern South America.

Kenk's (1930) definition of *Cura* refers only to the distribution of the testes, in that they extend only to the pharyngeal region, and makes no mention of their small number. In the diagnosis immediately following, he states that the testes are dorsal to the intestine. However, in his revision Kenk fails to mention at all the *Planaria pinguis* of Weiss (1910), which generally is acknowledged as belonging to *Cura*, and which has ventral testes. This error was perpetuated in the definition of the genus provided by Marcus (1946: 142, 173). The latter author also included in the genus a new species, *Cura schubarti*, in which the numerous testes extend to the bursa copulatrix. Previously, and on the basis of the original description only, I suggested that *C. schubarti* should be transferred to the genus *Dugesia* Girard, 1850 (Ball, 1971).

In 1955, Marcus described three new species of freshwater triclads from South Africa, and assigned them to *Cura*, thus extending the geographical range of the genus. The three species formed a uniform group and differed from other members of the genus in that they possessed very numerous testes and also reversed musculature of the bursal stalk, the circular layer of which was especially thick in *C. paeta* and *C. tinga*. At the same time, Marcus transferred *Planaria jeanneli* de Beauchamp, 1913, another species not considered by Kenk (1930), to the genus *Cura*.

These are the limits of the genus as recognized by most workers, and they form the basis of the recent definition proposed by Kawakatsu (1969a). The difficulties of precise definition are emphasized by some inadequacies in Kawakatsu's attempt, notably in his use of the phrase 'testes few', which is hardly applicable to the African species, and by his inclusion of 'penis with ... single bulbar cavity', which excludes *Cura pinguis*, the very species that he is discussing!

That the genus *Cura* is not a natural assemblage was first suggested by de Beauchamp (1961), and later he dropped the generic name altogether (de Beauchamp, 1968). In a recent review of the freshwater triclads I took a view very similar to that of de Beauchamp (Ball, 1974a). My approach was conservative in that I divided the genus *Dugesia* Girard, 1850, into a number of subgenera, the genus *Cura* also being divided and its parts relegated to subgeneric rank within *Dugesia*. Unfortunately, the publication of this review, which was completed in 1970, was delayed for reasons beyond my control, and I am now of the opinion, following further research and exchange of ideas, that most subgenera proposed there should rank as full genera and that the genus *Cura* should stand, albeit in a restricted sense.

With the acquisition of new data concerning certain known species, it is now possible to present an overview of *Cura* and similar forms in greater detail than before. The phylogenetic and biogeographical background to the taxonomic decisions made are discussed in detail elsewhere (Ball, 1974a), but with three major differences. In that study, I drew attention to the inadequate description of *Cura falklandica* (Westblad, 1952), but I suggested that it belonged with the other New World *Cura* species; and I have assigned *Cura schubarti* (Marcus, 1946) to the genus *Dugesia*, subgenus *Girardia* (Ball, 1974a). *Planaria jeanneli* de Beauchamp, 1913 proved to be a problematical species and was assigned tentatively to the subgenus *Dugesia* pending further study. More recently I have had the opportunity of examining

the type material of all these species, and as I find their closest relationships to be with African and Australasian forms they are transferred to the genus *Neppia* Ball, 1974a.

The discovery of two new *Cura* – like planarians from freshwaters in Tasmania emphasizes the necessity for a general review of the group. I have described the two new species in detail, and, moreover, have attempted to assemble in the present paper all pertinent taxonomic data on the described species previously assigned to *Cura* s.l. I add many new data and have re-examined relevant type material and made emendations and corrections to the original descriptions wherever necessary and possible. For a number of species without holotypes, designations of lectotypes have been made.

Cura foremanii was designated as type of a new family by von Graff (1916), but this was based on a misunderstanding of the description by Curtis (1900). In my earlier paper (Ball, 1974a) I erected a distinct family, the Dugesiidae, to contain all the *Cura*-like and *Dugesia*-like planarians assigned formerly to the Planariidae, and a detailed discussion of my reasons is contained therein. All known Australian, South African and South American Paludicola belong to this family (Ball, 1974a; 1974b).

Materials and Methods

Details concerning the sources and present locations of the specimens studied for this revision are given under the appropriate species headings. Specimens in the collections of the Department of Entomology and Invertebrate Zoology, Royal Ontario Museum, are assigned a catalogue number prefaced by ROM.

Specimens collected by me, or on my behalf, were killed in Steinmann's fluid (Steinmann and Bresslau, 1913) and fixed in 70 per cent ethanol, or they were killed and fixed in Carnoy's fluid from which the ether component was omitted. For sections, selected specimens were embedded in paraffin wax and serially sectioned at 8 μ m intervals. Thinner or thicker sections occasionally were cut for special purposes. The sections were mounted on 75 \times 50 mm glass microslides, the first section on each slide being in the top left-hand corner when the slide label is to the right. Frontal sections were arranged with the ribbons running horizontally; the sagittal and transverse sections were arranged with the ribbons vertical. The sections were stained with Mallory-Heidenhain stain, with Harris's Haematoxylin and Eosin, or with Phosphotungstic Acid Haematoxylin, and mounted in DPX (BDH Chemicals, Toronto).

All drawings from sections were made with the aid of a camera lucida; other drawings are free-hand. A calibrated ocular micrometer was used to make the measurements.

Systematic Section

Romankenkius gen. nov.

Diagnosis

Pigmented, with two eyes each composed of several pigment cells and numerous retinal cells. Head rounded, with auricular slits, without auricular lobes. Pharynx not pigmented. Testes large, numerous but discrete, dorsal or ventral, and prepharyngeal. Penis large, with seminal vesicle, without diaphragm in the ejaculatory duct, and asymmetrically placed in atrium. Bursa copulatrix situated laterally or anteriorly to penis. Bursal stalk with posterior diverticulum which receives the shell glands, and the oviducts separately or combined. Bursal stalk musculature of inner longitudinal and outer circular fibres. Cocoon unknown. Inhabitants of freshwater.

Type Species

Romankenkius kenki sp. nov.

Etymology

The genus is named for Dr. Roman Kenk in recognition of his meticulous and distinguished work on freshwater triclads over a period of fifty years, and in gratitude for his encouragement of my own work. Gender: masculine.

Key to the Species of the Genus *Romankenkius*

1. Testes dorsal; penis with prostatic vesicle *R. kenki* sp. nov.
Testes ventral; penis without prostatic vesicle *R. pedderensis* sp. nov.

Romankenkius kenki sp. nov.

Type Material

Department of Entomology and Invertebrate Zoology, Royal Ontario Museum. Holotype: sagittal sections on nine slides (ROM Cat. No. C9). Paratypes: sagittal sections of a specimen not fully mature on eleven slides (ROM Cat. No. C10); transverse sections on twelve slides (ROM Cat. No. C11); four specimens in alcohol (ROM Cat. No. C31). On one occasion an error was made in the ordering of the sections of the slide. The correct order of the sections on this particular slide (ROM Cat. No. C9, slide 3) has been marked clearly on the coverslip for the benefit of future students of this material.

Distribution

The type locality is a headwater to Lake Seal on the Rodway Range, Mt. Field National Park, Tasmania, 42°40' S 146°35' E. There is a gentle flow among large stones and granitic grit. Anaspids (Syncarida) are common in the lower stretches and embayments, together with gammarids (Amphipoda) and plecopterans (Insecta) in the swifter parts. Specimens collected 13 January 1972 by H.B.N. Hynes. Known only from the type locality.

Etymology

The species is named for Dr. Roman Kenk.

General Features (Fig. 1A)

Maximum size of preserved animals 13×6.15 mm. Dorsal surface uniform grey-brown to black; ventral surface paler. Head rounded, without traces of projecting auricles. Two small eyes situated close to the anterior margin, about equidistant from each other and their respective body margins. There is a small unpigmented area surrounding each eye. Marginally, and level with the eyes or just posterior to them, there are unpigmented sensory grooves. In the largest specimen the gonopore is 3 mm and the pharyngeal pore 4.5 mm from the posterior end. In many of the specimens there are irregularities in the pigmentation at the anterior and posterior margins. Serial sections indicate that most probably these are pathological.

Bodywall (Fig. 2A)

The dorsal epithelium is largely unciliated, nucleate, and packed with rhabdites. Beneath the thick basement membrane there are circular, diagonal, and longitudinal muscle fibres. The dorsal pigment is closely associated with the musculature and, in all but tangential sections, obscures the details of its arrangement. Beneath the dorsal musculature there are numerous cyanophil glands which are interpreted as rhabdite-forming glands.

The ventral bodywall is constructed similarly, but the epithelium is ciliated and has fewer rhabdites. The pigment is less dense, and the longitudinal muscle layer is particularly well developed. A group of eosinophil gland cells, probably of adhesive function, pierce the ventral bodywall medially-subterminally at the anterior end.

Sense Organs (Fig. 2A)

The principal sense organs are the anterior auricular slits and the eyes. In the entire animal the sensory pits may be recognized as depigmented areas situated laterally to and level with, or just behind, the eyes (Fig. 1A). The sensory epithelium is thin and is clothed with numerous very long cilia. These latter also occur in the immediately surrounding epithelium (Fig. 2A). Unusual in planarians is the fact that the sensory epithelium is not infra-nucleate; it contains normal nuclei. Rhabdites are lacking in and around the sensory slit. Beneath the sensory epithelium there is a strong concentration of nervous tissue, and the subepidermal pigment is lacking.

The two eyes are of the *Dugesia gonocephala* type as described and defined by Hesse (1897). Each consists of a pigment cup comprising several cells and embracing numerous visual or retinal cells (cf. Fig. 2D). The cup is orientated with the opening facing dorsolaterally, and the eyes are situated very close to the dorsal epithelium. The unpigmented area surrounding each eye is small, being not much larger than the eye itself, and the epithelium over the eyes still contains numerous rhabdites.

Alimentary System

The pharynx of *Romankenkius kenki* is of the normal planariid type and contains all the usual epithelial, muscular, nervous, and glandular zones

(Fig. 2C). Beneath the ciliated and infranucleate outer epithelium there is a layer of longitudinal muscle fibres. Beneath these there is a thick diffuse layer of circular fibres interspersed with numerous nuclei, which probably belong partly to the muscle fibres and partly to the epithelium. The central core comprises three zones: an outer glandular one, a central zone of nervous and glandular elements, and an inner glandular zone. Then follows the inner longitudinal musculature and a thick circular muscle zone. The inner musculature is similar to that of the outer layers except that it is more strongly developed. The pharyngeal structure thus is very similar to that of other aquatic triclads (von Graff, 1912–1917; Steinmann and Bresslau, 1913). The major difference lies in the fact that the circular muscle zones have extended inwards to encompass the zone of epithelial nuclei.

The intestine is typical of the group and shows no unusual features apart from the genito-intestinal communication described below. The number of intestinal diverticula was not determined. The anterior ramus of the intestine extends forwards to the level of the eyes, but there are no pre-ocellar diverticula.

Female Reproductive System (Fig. 3A)

The paired ovaries are relatively small oval bodies lying ventrally, above the nerve cords, just behind the brain, and far behind the eyes. The oviducts arise from the outer side of the ovaries and follow a somewhat sinuous course, laterally and above the nerve cords, to the level of the gonopore. Here they turn mediad and dorsad towards the distal part of the glandular duct, and just before entering the latter they combine to form a very short common oviduct. Throughout their length the oviducts communicate with the vitellaria. These latter are weakly developed in the specimens available for study, but they occur both dorsally and ventrally to the intestine.

The bursa copulatrix is a large sacciform and irregularly lobed organ lying to the left of the copulatory apparatus. It is lined with a tall nucleate epithelium, the cells of which have few inclusions, and which is bounded by a thin layer of muscles. Apparently these muscle fibres are derived partly from the mesenchymal musculature and partly from the musculature of the bursal stalk. There is a communication between the left lateral wall of the bursa copulatrix and the lumen of the adjacent intestinal branch. The bursal stalk arises from the posterior medial (right) side of the bursa copulatrix. It is a fairly wide duct which curves downwards to the left of the genital atrium and opens into the left wall of the latter, just above the gonopore, and in doing so forms a distinct common atrium. The bursal stalk is lined with a ciliated, nucleate columnar epithelium which is overlain by a thin layer of longitudinal muscle fibres and an outer, thicker layer of circular fibres. Overall, the musculature is not excessively developed. The ciliation is reduced towards the atrium. Numerous mesenchymal glands pierce the bursal stalk for its entire length.

The posterior diverticulum of the bursal stalk is a wide duct which originates from a point quite high on the bursal stalk above where it enters the atrium. In structure it is similar to the bursal stalk, but the epithelium is cuboidal, not columnar, and appears to be free of cilia. The posterior part of the diverticulum is pierced by numerous and extensive shell glands, and

distally to these it receives the very short common oviduct, as described previously.

Male Reproductive System (Figs. 2B, 3):

The testes are numerous but discrete, dorsoventrally large, and slightly irregular in shape. They are arranged in two or more rows lateral to the principal nerve cords, and they extend from behind the ovaries to, or just beyond, the pharyngeal root. The follicles occur between or above the gut diverticula, but they are principally dorsal in position (Fig. 2B).

The genital atrium is large and clearly divided into a male atrium housing the penis, and a common atrium formed by the ectal part of the bursal stalk at its junction with the male atrium. The single ventral gonopore opens to the common atrium. The male atrium is lined with a nucleate epithelium which is cuboidal ventrally and clavate dorsally. The epithelium is underlain by a thin layer of circular and then longitudinal muscle fibres.

The penis is massive and very muscular. The hemispherical bulb is embedded in the anterodorsal wall of the atrium, somewhat to the left of the midline, so that the penis is orientated asymmetrically (Fig. 3B). The penis papilla forms a very broad cone projecting posteriorly and diagonally, and there is a deep fold around the base of the papilla such that the lip of the fold projects towards the distal tip of the penis. The papilla is covered with a flat, nucleate, epithelium, becoming columnar entally, which is underlain by circular and longitudinal muscle fibres. The musculature of the ventral lip is particularly well developed.

Within the penis there are two distinct cavities of unusual relationship. What appears to be, from a functional viewpoint, a prostatic vesicle forms a large ovoid chamber, richly supplied on the dorsal surface with eosinophil glands, and occupying the basal and medial part of the papilla. This prostatic vesicle is lined with a very tall and nucleate epithelium, outside of which there are longitudinal and strong circular muscle fibres. Distally this narrows and receives the ejaculatory duct which opens at the tip of the penis papilla. Dorsally to the prostatic vesicle there is an elongate and thin-walled seminal vesicle. This commences in the penis bulb as a wide duct, narrows distally, and runs above the prostatic vesicle to open into the lumen of the latter at its distal end (Fig. 3A), thus forming the common ejaculatory duct. The seminal vesicle and its duct are lined with a low nucleate epithelium which is overlain by a thin muscle coat composed principally of longitudinal fibres.

The vasa deferentia open into the seminal vesicle in an asymmetric fashion (Fig. 3A). At the level of the pharyngeal pore the vasa deferentia, which are medial to the ventral nerve cords, enlarge to form false seminal vesicles. These run to the level of the male atrium before recurving towards the penis bulb. At this point they become once more thin tubes. The right vas deferens follows closely the vertical curvature of the anterior face of the penis bulb and pierces the latter so as to enter the frontal face of the seminal vesicle. The left vas deferens on the other hand, follows the vertical curvature of the left lateral face of the penis bulb and pierces the latter so as to enter the left lateral face of the seminal vesicle. These unusual courses of the vasa deferentia undoubtedly are a function of the asymmetric position of the penis within the male atrium.

Differential Diagnosis

Romankenkius kenki may be distinguished from the other known species of the genus by its possession of both a large prostatic vesicle and a small seminal vesicle. It differs also from the following species in its dorsal testes.

***Romankenkius pedderensis* sp. nov.**

Type Material

Department of Entomology and Invertebrate Zoology, Royal Ontario Museum. Holotype : sagittal sections on two slides (ROM Cat. No. C12). Paratypes: four sets of sagittal sections (ROM Cat. Nos. C13, C14, C18, C19); two sets of transverse sections (ROM Cat. Nos. C15, C16); one set of frontal sections (ROM Cat. No. C17).

Distribution

The type locality is Lake Pedder, Tasmania, 42°55' S 146°07' E. Lake Pedder is a small, acid lake in southwestern Tasmania. There are a significant number of aquatic invertebrates endemic to the lake, and a detailed account of the locality is given by Johnson (1972). Specimens collected from beneath stones, 11 March 1972, by I.A.E. Bayley. Known only from the type locality.

Etymology

The specific epithet refers to the type locality.

General Features (Fig. 1B)

Maximum size of preserved animals 8×2 mm. Dorsal surface uniform grey brown; ventral surface paler. The species is more slender than *R. kenki* and the two eyes are closer to the anterior margin.

Bodywall

The construction is basically as described for the preceding species, but the subepidermal pigmentation is less dense.

Sense Organs

The anterior sensory slits are similar to those of the preceding species (Fig. 2A), but they are somewhat smaller and more pit-like. The eyes (Fig. 2D) are as described for *R. kenki*.

Alimentary System

The pharynx is as described for *R. kenki* (Fig. 2C), but the total thickness of the pharyngeal wall is about two thirds of the size given. The various tissue layers, however, have the same proportional thicknesses. The intestine is typical of the group, apart from the genito-intestinal communication to be described below.

Female Reproductive System (Figs. 4A, C)

The small paired ovaries lie ventrally above, or medial to, the ventral nerve cords. They lie far behind the eyes and the cerebral ganglia (Fig. 1B). The

oviducts arise from the lateral walls of the ovaries and travel above the ventral nerve cords to the copulatory apparatus. The vitellaria are extensive, full of inclusions, and occur both dorsally and ventrally to the intestine. They begin anteriorly to the ovaries and are distributed almost to the posterior end of the animal.

The bursa copulatrix is a small spherical and lobed organ lying between the penis and the pharyngeal cavity, or to the left of the penis. From the left side of the bursa there extends a long bursa-intestinal duct which communicates with the lumen of the left posterior intestinal ramus (Fig. 4A). The bursal stalk arises from the posterior wall of the bursa copulatrix, sometimes undergoing a peculiar twist as it does so, and runs as a fairly narrow tube over and to the left of the copulatory apparatus. It broadens ectally and opens into the left lateral wall of the genital atrium, just above the gonopore, and it is from this point that the narrow posterior diverticulum, or glandular duct, projects ventroposteriorly. The shell glands are extensive and open into the bursal stalk diverticulum for almost its entire length. The oviducts open separately into the distal end of the diverticulum, but before doing so they extend a very short ventral branch towards the posterior vitellaria (Figs. 4A, C).

Histologically, the female reproductive system is, in all essentials, very similar to that of *R. kenki*.

Male Reproductive System (Fig. 4)

The testes are numerous, discrete, and somewhat smaller than those of the preceding species. They are arranged in two or more rows on each side of the animal, straddling the ventral nerve trunks. The first testes lie somewhat posteriorly to the ovaries, and the zone of the testes extends as far as the pharyngeal root (Fig. 1B). There are 10 to 15 follicles on each side. The follicles are principally ventral in position.

The penis is very large and muscular, and because it is positioned so asymmetrically in the male atrium, no true sagittal sections of this organ were obtained. The massive muscular bulb is embedded in the right side of the atrium and extends round to the frontal face (Fig. 4B). The large and broadly conical papilla thus projects diagonally across the animal, pointing ventrally towards the gonopore (Fig. 4C). The right vas deferens curves around the right side of the penis bulb and enters its right lateral face. The left vas deferens follows a unique course. Immediately posterior to the plane of the pharyngeal pore it turns mediad and passes behind the bursa copulatrix, beneath the bursal stalk, and around the frontal face of the penis bulb. It enters the latter separately from, and anterior to, the right vas deferens (Fig. 4A). Within the bulb the two vasa deferentia unite to form a slender pear-shaped seminal vesicle, and from this the narrow ejaculatory duct runs to the tip of the penis papilla. The papilla is richly supplied with eosinophil glands which open into the ejaculatory duct, seminal vesicle, and also into parts of the penial walls, especially the free dorsal part. In some specimens (Fig. 4B) the walls of the penis are folded to form well-developed lips, and frequently these too are richly supplied with eosinophil glands. In other respects, the histology of the male apparatus is similar to that of *R. kenki*.

Differential Diagnosis

Romankenkius pedderensis may be distinguished from the other species of the genus by its ventrally located testes and by the unique course of the vasa deferentia. It differs also from *R. kenki* in its lack of a prostatic vesicle.

Additional Remarks

The histological condition of the type series of *R. pedderensis* is not perfect, and consequently it is essential to study several sets of slides to observe all the important characters. In the sets of slides represented by ROM Catalogue Nos. C16–C19 an error was made by me during processing which has resulted in a mercuric precipitation on the sections. Whereas aesthetically this is not pleasing, it does not obscure the essential structure of the sections. It is noted here so that other taxonomists who may wish to use these reference slides will not be misled by these artifacts.

Discussion of the Genus *Romankenkius*

The high degree of asymmetry in the male copulatory organ and its associated ducts seen in these Tasmanian species is most unusual in the aquatic triclad. The prostatic vesicle of *R. kenki* is unique within this group, although such organs are of general occurrence in other Turbellaria and in some Cestoda (Hyman, 1951). A free, as opposed to interpolated, prostatic vesicle is known from polyclads of the families Stylochidae and Pseudoceridae (Bock, 1913; Hyman, 1951). Histologically the vesicle of these polyclads shows some similarities with that of *R. kenki*. In *Meixneria*, *Stylochus*, and *Pseudoceros*, for example, the large prostatic vesicle is lined with a tall epithelium overlain by a thick muscular coat, the whole being pierced by numerous glands. In the polyclads, however, the musculature consists of intermingled layers of circular and longitudinal fibres, whereas in *R. kenki* the musculature is reduced and consists of two layers. Furthermore, in *R. kenki* the seminal vesicle and its duct are situated dorsally to the prostatic vesicle and not ventrally as in the polyclads. Finally, in *R. kenki* the glands of the prostatic vesicle are largely confined to the dorsal wall and are not distributed over the entire surface as in, for example, *Meixneria* (Bock, 1913: Textfig. 11).

Originally it had been my intention to define *Romankenkius* on the basis of the prostatic vesicle, but the subsequent discovery of *R. pedderensis* negated this intention. I attribute much more importance to the unusual arrangements of the bursal stalk, oviducts, and shell glands. These are the same in both species, and their phylogenetic significance will be dealt with more fully in the General Discussion at the end of this paper.

Cura Strand, 1942 sensu stricto

Diagnosis

Pigmented, with two eyes, each composed of several pigment cells and

numerous retinal cells. Head truncate, or of low triangular form, with definite auricular streaks. Pharynx not pigmented. Testes small, discrete and very few in number, preoral, dorsal or ventral to intestine. Seminal vesicle present or absent; without a diaphragm in ejaculatory duct. Bursa copulatrix present or absent; if present situated anteriorly to penis. Oviducts empty into bursal stalk, or female genital canal, above zone of the shell glands. Bursal stalk musculature of inner circular muscles surrounded by a fine and discontinuous layer of longitudinal fibres. Atrium usually divided in that the vagina, receiving the shell glands, is expanded into a female atrium. Cocoon stalked. Inhabitants of freshwater.

Type species

Cura foremanii (Girard, 1852).

Key to the Species of the Genus *Cura*

1. Bursa copulatrix present; without genito-intestinal communication; testes pre-pharyngeal 2
 Bursa copulatrix absent; genito-intestinal communication present; testes extend to mouth *Cura foremanii*
2. Sensory fossae on anterior margin; atrium muscularized; seminal vesicle absent; testes ventral *Cura pinguis*
 No sensory fossae; atrium normal; seminal vesicle present; testes dorsal 3
3. Up to 4 testes on each side; atrium without pockets *Cura azteca*
 Up to 9 testes on each side; atrium with pockets 4
4. Common oviduct opens to bursal stalk *Cura michaelsoni*
 Oviducts open separately into bursal stalk *Cura patagonica*

Cura foremanii (Girard, 1852)

Dugesia Foremanii Girard, 1852: 210.

Planaria foremanii – Stringer, 1918: 355.

Curtisia foremanii – Hyman, 1931: 322.

Cura foremanii – Marcus, 1955: 111.

Dugesia (Cura) foremanii – Ball, 1974a: 377.

Planaria simplissima Curtis, 1900: 447.

Curtisia simplissima – Kenk, 1930: 290.

Planaria simplicissima – Stevens, 1907: 350 (lapsus calami).

Curtisia simplicissima – von Graff, 1916: 3213.

Planaria lugubris – Morgan, 1901, et auct. (non Schmidt, 1862).

Planaria polychora – Kepner and Pickens, 1925: 237 (non *P. polychroa* Schmidt, 1862).

Type Material

Location unknown.

Distribution

Eastern North America (Ball, 1969; Kenk, 1972).

Material Examined

Numerous living and preserved specimens, and sections, from Ontario,

Quebec, New Brunswick, Prince Edward Island, Nova Scotia, Newfoundland, Maine, New York, and Pennsylvania. Material now in the collections of the National Museum of Natural Sciences, Ottawa, and the Department of Entomology and Invertebrate Zoology, Royal Ontario Museum. The specimens are held as serial sections or preserved specimens in alcohol.

Remarks

Detailed descriptions have been provided by Curtis (1900) and Kenk (1935, 1944). The copulatory organs of this, the type species of the genus, are also shown in Fig. 5D. There are up to five testes on each side, situated dorsally, and distributed posteriorly as far as the mouth. A bursa copulatrix is always absent and is replaced by a ductus genito-intestinalis. *C. foremanii* also is unique within the genus in that it reproduces by self-fertilization (Anderson, 1952; Anderson and Johann, 1958). The large spherical and muscular seminal vesicle within the penis bulb seems also to distinguish this species from most others in the genus.

C. foremanii is the only species of the genus known from North America. Ball and Fernando (1969) referred to a species from Canada yet to be described. I now refer the specimens in question (ROM Cat. C84) to the present species, even though they show certain peculiarities in the copulatory apparatus. The original collectors were unsure of the exact collecting locality in New Brunswick, and my own intensive collecting at the most probable sites has failed to yield further specimens with these particular peculiarities.

Cura patagonica (Borelli, 1901)

Planaria patagonica Borelli, 1901: 1.

Curtisia patagonica – Kenk, 1930: 290.

Euplanaria patagonica – de Beauchamp, 1939a: 72.

Cura patagonica – Marcus, 1955: 111.

Dugesia (*Cura*) *patagonica* – Ball, 1974a: 377.

Type Material

Location unknown.

Distribution

Rio Santa Cruz, Patagonia, Argentina.

Material Examined

None. Known only from the original description.

Remarks

This species is considered to be identical with *C. michaelsoni* by de Beauchamp (1939a). Böhmig (1902) studied both species and considered them to be distinct. *C. patagonica* is unusual in its possession of two lateral pouches of the atrium and because it has more testes, up to nine follicles on each side, than the other species of the genus. The testes are prepharyngeal. The epithelium of the bursal stalk was described as being separated from the sur-

rounding connective tissue by weak layers of longitudinal and circular fibres (Borelli, 1901: 4). If it is inferred from this that the outer layers are the circular ones, then the species may have to be transferred to *Neppia*. I defer such a decision until further material is available to resolve the problem.

***Cura michaelsoni* (Böhmig, 1902)**

Planaria michaelsoni Böhmig, 1902: 20.

Curtisia michaelsoni – Kenk, 1930: 290.

Euplanaria michaelsoni – de Beauchamp, 1939a: 72.

Cura michaelsoni – Marcus, 1955: 111.

Cura michaelsoni – Ball, 1969: 60 (lapsus calami).

Dugesia (Cura) michaelsoni – Ball, 1974a: 377.

Type Material

Location unknown.

Distribution

Isla Picton, Tierra del Fuego, Chile.

Material Examined

None. Known only from the original description.

Remarks

This species is remarkably similar to *C. patagonica*, especially in its possession of the two lateral pouches of the atrium. Böhmig (1902) does not describe the histology of the bursal stalk, but judging from his Fig. 37 the musculature is weak and with outer longitudinal fibres. This indicates that the species probably does belong in the genus *Cura* s.s. On the other hand, the ejaculatory duct shows some dilations and foldings that are reminiscent of the condition usual in the genus *Neppia*, and especially in *N. montana*. As with *C. patagonica*, I suspect that this species, upon re-examination, will be found not to be a true *Cura* species. The oviducts open into a single duct that empties into the posterior wall of the base of the bursal stalk. This duct, or “Drusengang” (Böhmig, 1902: Fig. 37), seems similar to the posterior diverticulum of the bursal stalk of the new genus *Romankenkius*, except that it does not receive the shell glands. Instead, the shell glands open ectally and entally, principally the latter, to the “Drusengang”. This is an unusual arrangement, and it serves to distinguish *C. michaelsoni* from *C. patagonica*.

***Cura pinguis* (Weiss, 1910)**

Planaria pinguis Weiss, 1910: 546.

Euplanaria pinguis – de Beauchamp, 1940a: 319.

Curtisia stagnalis Nurse, 1950: 414.

Cura pinguis – Marcus, 1955: 111.

Dugesia pinguis – de Beauchamp, 1951a: 94; 1968: 67.

Dugesia (Cura) pinguis – Ball, 1974a: 377.

Type Material

Department of Entomology and Invertebrate Zoology, Royal Ontario Museum (Lectotype: sagittal sections on 20 slides, ROM Cat. No. C85). Zoological Institute, Graz, Austria (Paralectotype: transverse sections on 5 slides).

Distribution

Australia; New Zealand; New Caledonia; possibly Java (see Kawakatsu, 1969a). New records: Tasmania, New Zealand (North Island).

Material Examined

Type material, as above. Living and preserved material and serial sections of specimens from: AUSTRALIA. Shannon River, Hermitage, Tasmania ($42^{\circ}15' \text{ S } 146^{\circ}53' \text{ E}$), 16 January 1972, H.B.N. Hynes (ROM Cat. No. C100); Kentucky Creek, Uralla, New South Wales ($30^{\circ}40' \text{ S } 151^{\circ}31' \text{ E}$), 15 November 1972, L.R. Richardson (ROM Cat. No. C99, C101); Crown Creek, Woods Point, Victoria ($37^{\circ}36' \text{ S } 146^{\circ}42' \text{ E}$), 25 August 1971, H.B.N. Hynes (ROM Cat. No. C98); Lake Kerford and King River, Beechworth, Victoria ($37^{\circ}36' \text{ S } 146^{\circ}42' \text{ E}$), June–July 1973, D.A. Hay (ROM Cat. No. C71, C73). NEW ZEALAND. Marley's Pond, Christchurch, South Island ($43^{\circ}35' \text{ S } 172^{\circ}40' \text{ E}$), 9 February 1942, F. R. Nurse (Mrs. F.R. Allison) (ROM Cat. No. C103); a domestic well, Taumarunui, North Island ($38^{\circ}53' \text{ S } 175^{\circ}16' \text{ E}$), 1972, G.A.H. Helson (ROM Cat. No. C102).

Remarks

The only surviving type material is that cited above. I have selected the series of sagittal sections to be the lectotype; these appear to be the slides upon which Fig. 32 of Weiss (1910) is based, which latter is a mirror image of the actual sections.

Detailed descriptions of *Cura pinguis* have been provided by Weiss (1910), Nurse (1950) and Kawakatsu (1969a, 1969b). In common with many other Australasian freshwater planarians, *C. pinguis* possesses sensory fossae on the frontal margin. Four such fossae on each side have been described in specimens from Western Australia (Weiss, 1910) and New Caledonia (Kawakatsu, 1969a). These fossae are not always visible in entire preserved specimens, but they are easily detected in sections, and all my observations agree with those cited above. This suggests that the number of fossae is constant and diagnostic of the species, which lends credence to de Beauchamp's identification of immature specimens from Java as *C. pinguis* (de Beauchamp, 1929). A histological description of the fossae was provided by de Beauchamp (1929).

Anatomically this species is readily recognized by the strong musculature surrounding the male atrium, by the high cushion cells lining the latter, and by the finger-like penis papilla. The general facies of the copulatory apparatus is most similar to that of *C. foremanii*, but it lacks a true seminal vesicle. The number of testes is greatly reduced, there being one or two follicles only on each side, and they are situated ventrally, a condition unique within the genus. The testes are prepharyngeal. Nurse (1950) describes a long common vas deferens entering the penis bulb. I cannot trace the vasa deferentia in my material from Christchurch, New Zealand, but in all the other sections

it is clear that they enter separately the walls of the penis bulb, sometimes enlarging before they do so (Fig. 5C).

The bursal stalk musculature, a character to which I have attached great taxonomic importance (Ball, 1974a), is very difficult to interpret in this species because it is so weakly developed. In the published descriptions there have been differences of opinion (see Ball, 1970; 1974a). In none of my material can I detect longitudinal fibres immediately beneath the epithelium, but the circular fibres are easily seen. In the lectotype there do not appear to be outer longitudinal fibres ectally, but there are scattered longitudinal fibres in the ental region. In the other specimens, outer, but very weak and scattered, longitudinal fibres can be detected over most of the bursal stalk. However, as with *C. foremanii*, optimal staining is essential for the histological interpretation of the female genital ducts.

Kawakatsu (1969a) has drawn attention to infraspecific geographical variation in this species. I agree that *C. pinguis* is polymorphic, and like *Dugesia tigrina* in North America, is probably in the process of forming new races. Indeed, it may already represent a complex of closely related species. I have observed living animals from New South Wales and could easily distinguish with the naked eye two morphological types (Fig. 5A, B), but I could not correlate these types with any consistent differences in their copulatory apparatus. Both types possessed definite auricles, but this is not the case in the specimen figured by Nurse (1950: plate 45, fig. 4a). The specimen illustrated in my Fig. 5B is also superficially similar to some '*Dugesia*' species I have received from Australia. None of these are mature, but they are easily distinguished by their pigmented pharynx. In the majority of my specimens of *C. pinguis* there is a bursa copulatrix, but in those from Christchurch, New Zealand, it is absent. In the specimens from Taumarunui, New Zealand, the bursal stalk is acutely flexed as described by Weiss (1910: Fig. 32) and Kawakatsu (1969a: fig. 3; 1969b: fig. 2). In all the other specimens it is more smoothly curved as described by Nurse (1950: pl. 47, fig. 1). The material available is inadequate to elucidate these problems further, but a careful comparative study of *C. pinguis* over its entire range should prove most rewarding. The species is known from a wide variety of habitats including ponds and streams (Nurse, 1950), streams subject to partial drying and thus probably to wide temperature fluctuations (Kawakatsu, 1969b; specimens from New South Wales), from a fast flowing stream (Weiss, 1910), and from a domestic well (Taumarunui, N.Z.).

***Cura azteca* Benazzi and Giannini, 1971**

Cura azteca Benazzi and Giannini, 1971: 477.

Dugesia (*Cura*) *azteca* – Ball, 1974a: 377.

Type Material

Istituto de Zoologia e Anatomia Comparata, Universita di Pisa, Italy; three slides in the care of Professor Mario Benazzi.

Distribution

El Zarco, Puerta de las Cruces, Federal District of Mexico, Mexico.

Material Examined

None.

Remarks

This is another species with a large, though irregular, seminal vesicle. There are up to four testicular follicles on each side, and situated dorsally. They are prepharyngeal. The bursal stalk musculature is not described, but it is said to be of the *C. foremanii* type (M. Benazzi, pers. comm., 1972).

Discussion of the Genus *Cura*

It is still an open question as to whether or not the genus *Cura*, as restricted here, is yet a monophyletic assemblage. The inclusion of *C. patagonica* and *C. michaelsoni* needs final justification from a re-examination of these species. Unfortunately, I have been unable to trace the types, and I have not had access to any new material. It is possible that Böhmig's types were destroyed in the bombing of Graz in the Second World War (E. Reisinger, pers. comm., 1973). The following remarks, then, refer to the genus as represented by *C. pinguis*, and *C. foremanii*, the two species of which I have been able to study ample material.

With respect to the general anatomy and histology of the copulatory complex the genus *Cura* s.s. seems quite different from the other genera discussed in this paper. Apart from characters already discussed, the distinctness of the genus from *Neppia* and from *Romankenkius* gen. nov. is emphasized by two additional characters: the pharyngeal musculature, and the structure of the auricular sensory organs. With respect to these characters *Cura* s.s. is more similar to the New World *Dugesia* species than to the other austral planarians.

I have measured the pharyngeal musculature of all the species examined for this revision and I have found that in *Cura* s.s. the inner circular muscles represent between 8 per cent and 12 per cent of the total thickness of the pharyngeal wall, whereas in *Neppia* and *Romankenkius* gen. nov. the proportional thickness of this circular layer is 20 per cent–25 per cent, or about twice as much. The difference is constant and would be a good guide for the taxonomic placement of immature specimens.

Regarding the auricular organs, it may be noted that in both *C. foremanii* and *C. pinguis* these consist of a strip of modified epithelium which is well supplied with nerve endings. The principal modifications are reduction in cell height, loss of rhabdites, and loss of subepidermal pigment. But there is no deep folding of the epithelial wall such that a furrow or flask-shaped pit is formed. Such folding is usual in both *Neppia* and *Romankenkius* and in some other austral freshwater planarians (Weiss, 1910; Marcus, 1955; Ball, 1974b).

Biogeographically the occurrence of *Cura* s.s. in such widely disparate areas as North America and Australia seems puzzling. Possibly, and as argued previously (Ball, 1974a), this primitive genus originated on one of

the Gondwanian continents, and the present distribution reflects the persistence in time of relict peripheral populations. One would expect, however, to find intermediate forms, in South America for example, and this is why critical reassessment of *C. patagonica* and *C. michaelsoni* is so essential. The North American form, *Cura foremanii*, is restricted to cool creeks, and *Cura azteca* of Mexico was found in caves. Thus the genus *Cura* may be characteristically cold stenothermal, and suitable habitats have not often been sampled by workers in South America, vast areas of which, particularly west of the Andes, have not been studied.

***Neppia* Ball, 1974a**

Diagnosis

Pigmented, with two eyes, each composed of several pigment cells and numerous retinal cells. Head typically of low triangular form, with definite auricular slits. Pharynx usually free of pigment. Testes numerous, dorsal (except *N. tinga*) and not extending beyond copulatory apparatus. Seminal vesicle a single muscular cavity. Ejaculatory duct typically convoluted, usually with a proximal glandular chamber, and without a diaphragm. Bursa copulatrix present anterior to penis. Bursal stalk musculature of inner longitudinal fibres surrounded by a thick layer of circular fibres, particularly ectally. Oviducts enter bursal stalk above zone of shell glands. Cocoon so far as known, unstalked. Inhabitants of freshwater.

Type species

N. montana (Nurse, 1950).

Etymology

Named for Valeria Neppi for her many early contributions to our knowledge of the lower metazoa. Gender: feminine.

Key to the Species of the Genus *Neppia*

- | | |
|---|---------------------|
| 1. Head of high triangular form; testes extend to copulatory apparatus | 2 |
| Head of low triangular form; testes prepharyngeal | 3 |
| 2. Ejaculatory duct opens terminally; atrium with two lateral pouches | <i>N. schubarti</i> |
| Ejaculatory duct opens dorsally; atrium with single posterior diverticulum | <i>N. montana</i> |
| 3. Outer musculature of pharynx in three distinct layers | 4 |
| Outer musculature of pharynx in two distinct layers | 5 |
| 4. Bursal stalk acutely flexed, musculature very thick and exceeding diameter of lumen; epithelium of bursal stalk infranucleate; penis stout and blunt | <i>N. paeta</i> |
| Bursal stalk smoothly curved, with thinner musculature; epithelium of bursal stalk usually nucleate; penis more slender and pointed | <i>N. jeanneli</i> |
| 5. Testes principally dorsal | 6 |
| Testes ventral | <i>N. tinga</i> |
| 6. Atrium with thick musculature; bursal stalk with thinner muscles; with a short common oviduct | <i>N. evelinae</i> |
| Atrial musculature normal; bursal stalk musculature thick; oviducal openings separate | 7 |

7. Penis with marked basal fold and with small glandular chamber; oviducal openings asymmetric *N. wimbimba*
 Penis without basal fold and with large glandular chamber; oviducal openings symmetric *N. falklandica*

***Neppia montana* (Nurse, 1950)**

Dugesia montana Nurse, 1950: 412.

Dugesia (*Neppia*) *montana* – Ball, 1974a: 377.

Type Material

Canterbury Museum, Christchurch, New Zealand.

Distribution

Stewart Island and South Island, New Zealand.

Material Examined

Paratypes, as preserved specimens and serial sections, from Cass Stream, Christchurch, New Zealand. This material is now deposited in the collections of the Department of Entomology and Invertebrate Zoology, Royal Ontario Museum.

Remarks

This species, together with *N. schubarti*, is unusual within the genus in that the testes extend as far as the copulatory apparatus. The oviducts enter separately the frontal face of the bursal stalk (Ball, 1974a: fig. 9). The wide, sometimes folded, posterior diverticulum of the bursal stalk (Ball, loc. cit.) is quite unlike that of *Romankenkius* gen. nov. and may be a fixation artifact resulting from deformations caused by the very strong ectal musculature of the bursal stalk. In cross-section the bursal stalk is wide and dorsoventrally flattened, just as it is in *N. falklandica*. The phenetic similarity between the penis of *N. montana* (Ball, 1974a: fig. 9) and that of *C. michaelsoni* (Böhmig, 1902: Fig. 37) is quite striking. The many similarities between *N. montana* and *N. schubarti* will be discussed further below.

Nurse (1950) divided this species into two varieties, the status of which need further study.

***Neppia jeanneli* (de Beauchamp, 1913) comb. nov.**

Planaria Jeanneli de Beauchamp, 1913: 8.

Euplanaria Jeanneli – de Beauchamp, 1939a: 73; 1939b: 120.

Dugesia Jeanneli – de Beauchamp, 1951b: 81.

Cura jeanneli – Marcus, 1955: 111.

Dugesia (? *Dugesia*) *jeanneli* – Ball, 1974a: 376.

Type Material

Private collection of Professor P. de Beauchamp, Paris, France.

Distribution

Mt. Kilimanjaro, Tanzania.

Material Examined

Syntypes, as follows: one wholemount; sagittal sections of the postpharyngeal region on two slides; sagittal sections of the postpharyngeal region on one slide; sagittal sections of the prepharyngeal region on two slides; transverse sections of the postpharyngeal region on one slide.

Remarks

The original description by de Beauchamp (1913) was corrected at a later date (de Beauchamp, 1939a). The principal corrections were the recognition of a third layer of muscles in the outer musculature of the pharynx, and the observation that the oviducts open into the bursal stalk separately from the sides, not after union to form a common oviduct. In fact the oviducts open somewhat asymmetrically, as in *N. wimbimba*, in that the right oviduct opens more ventrally and more anteriorly than the left one. The unusual pharyngeal musculature compares with that in *Dugesia gonocephala* and its allies (Marcus, 1953; Dahm, 1967) and in *Neppia paeta*.

Determination of the affinities of this form has been made difficult as a result of a puzzling statement in de Beauchamp's later paper (de Beauchamp, 1939a: 37). Here de Beauchamp refers to the weak differentiation of the female apparatus. From the text following it seems that he is referring to the bursa and bursal stalk, as assumed by Marcus (1955: 111) and by me (Ball, 1974a: 378). This made it impossible to assign the species to the genus *Neppia*, and therefore I tentatively placed it in the subgenus *Dugesia* (Ball, 1974a: 376). A re-interpretation of the copulatory apparatus is given in Fig. 6A, and this shows that the female ducts are well developed and that the species can satisfactorily be classified with *Neppia* after all.

The strong ectal circular muscles of the bursal stalk are bounded by a re-inforcing layer of longitudinal muscles, just as in *N. evelinae*, *N. tinga* and *N. falklandica*, though here it is more strongly developed than in the other species. The bursa itself may be anterior to the penis, or it may be to the right side; it is somewhat tubular in shape. The bursal stalk passes over the copulatory apparatus and opens medially into the atrium, or a little to the left side. The epithelium of the bursal stalk is nucleate for the most part.

The ovaries and vitellaria are very weakly developed in all the available specimens; perhaps this is the basis of the statement of de Beauchamp discussed above. The numerous and small prepharyngeal testes are situated dorsally to the intestine. They are at an early stage of maturation and probably are much larger at maturity.

In one set of sagittal sections (two slides) the penis is as described by de Beauchamp (loc. cit.); it is shown in Fig. 6A. In the other set (one slide) the penis is contracted, lacks the epithelial fold, and possesses a folded ejaculatory duct which opens more ventrally than terminally (Fig. 6B). In this specimen the entire penis is very much like that of *N. paeta*. However, *N. paeta* is easily distinguished from *N. jeanneli* by its extraordinarily thick muscles of the bursal stalk, and by the acute flexure in the latter. In both sets of sagittal sections of *N. jeanneli* a spermatophore can be seen.

N. jeanneli is similar to *N. wimbimba* in its asymmetric oviducal openings and in their joint possession of a penial fold. But in *N. wimbimba* the penial fold is very strongly developed, as are the ectal muscles of the bursal stalk. The principal difference between the two resides in the fact that *N. wimbimba* does not possess the extra layer of longitudinal fibres in the outer musculature of the pharynx.

***Neppia schubarti* (Marcus, 1946) comb. nov.**

Curtisia schubarti Marcus, 1946: 142.

Cura schubarti – Marcus, 1955: 111.

Dugesia (*Girardia*) *schubarti* – Ball, 1974a: 377.

Type Material

Section of Invertebrate Zoology, Swedish Museum of Natural History, Stockholm, Sweden.

Distribution

Southern Brasil.

Material Examined

The type material available to me consists of: sagittal sections on three slides; transverse sections on three slides; frontal sections on two slides. These are without data and are regarded as syntypes. One other series of slides was examined: BRASIL. Riacho de Pedreira, Biological Station of Boraceia, State of São Paulo (23°42' S 45°48'W), 23 November 1966, M.E.Q. Martins (sagittal sections on 14 slides in the care of the Department of Zoology, University of São Paulo).

Remarks

A detailed description of this species has been provided by Marcus (1946). Although at that time the importance of the bursal stalk musculature was not realized, Marcus (1946: 145) refers to the fact that the circular fibres are especially strong, but whether or not the layers are reversed with respect to the atrium and bodywall is not made clear. By examination of the type material I have been able to observe the strong development of the muscles of the bursal canal and their reversal. In the light of this new data my assignment of *Curtisia schubarti* to the genus *Dugesia* subgenus *Girardia* was mistaken (Ball, 1971; 1974a); the species clearly belongs in *Neppia*.

The significances of some similarities of this species, and of *N. montana*, to those Nearctic and Neotropical planarians of the *Dugesia* (*Girardia*) *tigrina* group need further elucidation. All these forms have a high triangular head, apparently an apomorph or derived character (Ball, 1974a), and, from study of the material immediately available to me, it seems that *N. schubarti* may have a pigmented pharynx. From these data it is possible to infer that *Neppia* and *Girardia* have an ancestor in common more recently than either has an ancestor in common with *Cura* (cf. Ball, 1974a: fig. 11). While this possibility needs further investigation, it may be stated unequiv-

ocally that *N. schubarti* and *N. montana* form a well-defined subgroup within the genus.

***Neppia falklandica* (Westblad, 1952) comb. nov.**

Curtisia falklandica Westblad, 1952: 49.

Cura falklandica – Marcus, 1955: 111.

Dugesia (?*Cura*) *falklandica* – Ball, 1974a: 377.

Type Material

Section of Invertebrate Zoology, Swedish Museum of Natural History, Stockholm, Sweden.

Distribution

Port Stanley, Falkland Islands.

Material Examined

Lectotype. Westblad (1952) did not designate a holotype. I have selected one set of sagittal sections on five slides (SSP6, 1–5) to be the lectotype, and I have labelled the slides accordingly. These seem to be of the specimen from which Westblad's fig. 24B was drawn. Paralectotypes as follows: transverse sections on nine slides (II. 1–9); transverse sections of the copulatory apparatus on two slides (I, 1–2); transverse sections of the copulatory apparatus on one slide; frontal sections of the prepharyngeal region on two slides, and sagittal sections of the postpharyngeal region on one slide, all of a single specimen (SSP2) labelled as *Planaria* n. sp.

Remarks

Previously (Ball, 1974a) I commented on the inadequate original description of this species which made it impossible to assign the species to any genus or subgenus with certainty. The discovery that *N. falklandica* is closely related to freshwater triclad from South Africa and Australasia is of great biogeographical interest, and makes a reappraisal of such forms as *Cura michaelsoni* and *C. patagonica* (q.v.) an important task.

The pharynx is of the usual planariid structure and is similar to that of other species of *Neppia* and *Romankenkius*, but it does not possess the extra layer of longitudinal fibres in the outer muscle zone such as is found in *N. paeta* and *N. jeanneli*.

The testes are very numerous, up to 15 follicles on each side, dorsoventrally large, and distributed from just behind the ovaries to the pharyngeal root; they may be dorsal or ventral to the intestine, but principally they are dorsal. A re-interpretation of the copulatory apparatus is given in Fig. 6C which may be compared with Westblad's original figure (Westblad, 1952: fig. 24B). Unusual features are the large size of the glandular chamber forming the proximal part of the ejaculatory duct, the elongate nature of the penis bulb, and the courses of the vasa deferentia. At the penis bulb each vas deferens enlarges to form an ovoid false seminal vesicle. Similar, but much smaller, structures have been described for *N. wimbimba* and *N. tinga*.

These vesicles open via a narrow canal into the principal seminal vesicle within the penis bulb. The right one opens, as shown by Westblad (loc. cit.), from a dorsal situation, but the left one opens from a more ventral position as shown in Fig. 6C. The epithelia of the copulatory apparatus are nucleate throughout. The musculature of the atrium continues the sequence of the body wall, but over the bursal stalk it is reversed. Here the outer layer is of circular fibres, and these are very thick ectally and become thinner entally. Ectally there is re-inforcement with a few outer longitudinal fibres. The bursal stalk is not always smoothly curved; it may follow an irregular winding course over the copulatory apparatus. Numerous mesenchymal glands open into the bursal stalk.

Marcus (1955) considered *N. falklandica* to be almost identical with *N. tinga*. The male system does share some similarities with that of *N. tinga*, particularly in the distribution of the testes and in the glandular nature of the proximal part of the ejaculatory duct. However, the two species are quite distinct as is evidenced by the shape of the penis, the shape and course of the ejaculatory duct, and by the arrangements of the female ducts. *N. falklandica* is similar to *N. montana* from New Zealand, both in the form of the large penis with its irregular ejaculatory duct and sharply folded epithelium, and in the musculature of the bursal stalk (cf. Fig. 6C with Ball, 1974a: fig. 9).

***Neppia evelinae* (Marcus, 1955) comb. nov.**

Cura evelinae Marcus, 1955: 105.

Dugesia (? *Dugesia*) *evelinae* – Ball, 1974a: 376.

Type Material

Zoological Museum, University of Lund, Sweden. Kat. 1, typkat. 70.

Distribution

Cape Province, South Africa.

Material Examined

The type material available to me consists of eight slides comprising five sets of sagittal sections of the copulatory apparatus, one set of transverse sections of the copulatory apparatus and one of the pharyngeal region, and one set of sagittal sections of the prepharyngeal region. Many of the sections are in poor histological condition. Marcus did not establish a holotype. I have selected and labelled one set of sagittal sections to be the lectotype. This appears to be the slide from which Marcus drew his fig. 20. The remaining slides are paralectotypes.

Remarks

In my earlier study I found this species to be problematical. It did not seem to belong to *Cura* or *Neppia* as recognized therein (Ball, 1974a). Consequently I placed it provisionally with the group of *Dugesia* species exemplified by *D. gonocephala* and its allies, while stating that its status needed clarification.

After a careful study of the type material I have decided that the species is best classified with the genus *Neppia* after all. It is true that the bursal stalk musculature is not as powerfully developed as in the other species and is, in fact, less developed than in some Old World *Dugesia* species. But the musculature does show the ental diminution which is so characteristic of many other species of the genus. However, it is in penial anatomy that *N. evelinae* is most similar to the other species of the genus. The penis bulb is unusually elongate and very muscular, in which respects it is very similar to *N. falklandica*. The seminal vesicle opens into an enlargement of the proximal part of the ejaculatory duct which is supplied with many glands, as in *N. tinga*, *N. falklandica*, *N. wimbimba*, and to a lesser extent *N. paeta*. This penial structure (Marcus, 1955: fig. 20) is quite different from that found in the genera *Cura* s.s and *Romankenkius*. *N. evelinae* does not possess a diaphragm in the ejaculatory duct of the type found in *Dugesia gonocephala* (see Ball, 1974a), but the glandular dilation of the proximal part of the ejaculatory duct may be the phylogenetic precursor of such a structure.

The arrangement of the common oviduct and shell glands is unusual. I have confirmed that there is a short common oviduct which enters the posterior face of the bursal stalk as described by Marcus. The shell glands enter this common oviduct and also the lateroposterior walls of the bursal stalk in the vicinity of the oviduct. Histologically it is a true common oviduct in that the epithelial structure and surrounding musculature is more akin to that of the oviducts than to the bursal stalk. In *Romankenkius* gen. nov. the situation is quite different in that there is a large and distinct posterior diverticulum of the bursal stalk into which both the shell glands and the oviducts open.

Neppia evelinae has been compared with *Cura pinguis* in the form of the penis papilla and the atrial musculature (Marcus, 1955; Ball and Fernando, 1969). A close relationship between these two species now seems unlikely. *N. montana*, for example, also shows thickened atrial muscles (Ball, 1974a: fig. 9), and in both species the relationships between the atrial muscles and the muscles of the penis bulb are unlike those of *Cura pinguis* (cf. Marcus, 1955: fig. 20 with Weiss, 1910: Fig. 32). The penis papilla of *C. pinguis* is an extraordinarily weak and undifferentiated structure (Fig. 5C), whereas that of *N. evelinae* is much more muscular and complex. Moreover, the separation of *N. evelinae* from *Cura* s.s. is confirmed by the pharyngeal musculature and by the structure of the auricular organ (p. 17).

Neppia paeta (Marcus, 1955)

Cura paeta Marcus, 1955: 107.

Dugesia (*Neppia*) *paeta* – Ball, 1974a: 377.

Type Material

Zoological Museum, University of Lund, Sweden. Kat. 1, typkat. 71.

Distribution

Cape Province and Basutoland, South Africa.

Material Examined

The type material available to me consists of four slides. There is one set of frontal sections of the anterior end on one slide and one set of transverse sections of the medial region on one slide. The single slide of sagittal sections of the postpharyngeal region clearly is the basis of Marcus's (1955) fig. 27. These three slides appear to be separate sets of sections of the same animal. Each one of them is etched with the number 975.2, and they are here designated as the lectotype of *Neppia paeta*.

Remarks

From these slides I can add little to Marcus's excellent description, except to make good his omission of the observation that the testes are situated dorsally. The complete infranucleate state of the bursal stalk epithelium is unique within the group of species considered in this revision. In *N. schubarti* and *N. jeanneli* the same epithelium may be partly infranucleate.

The fourth slide, a set of sections of the postpharyngeal region of a small animal, is problematical. It is probably one of those immature specimens discussed by Marcus (1955: 109). The bursal stalk musculature is not especially thick, and this demonstrates the need to use fully mature specimens for reaching taxonomic decisions. In all these slides the extra inner layer of longitudinal muscles in the outer muscle zone of the pharynx is prominent. Such a layer is otherwise known only in *Neppia jeanneli* and in certain species of the *Dugesia gonocephala* group (de Beauchamp, 1939a; Dahm, 1967, 1971).

Neppia tinga (Marcus, 1955)

Cura tinga Marcus, 1955: 109.

Dugesia (*Neppia*) *tinga* – Ball, 1974a: 377.

Type Material

Zoological Museum, University of Lund, Sweden. Kat. 1, typkat. 72.

Distribution

Basutoland, South Africa.

Material Examined

The type material available to me consists of three slides. These are one set of sagittal sections of the postpharyngeal region, one set of sagittal sections of the prepharyngeal region, and one set of transverse sections through the pharyngeal region. Because all the slides appear to be from a single animal the entire set is designated as the lectotype.

Remarks

From a study of the sections of the copulatory apparatus I find that I cannot agree entirely with the reconstruction forming Marcus's (1955) fig. 31. In fact, accurate reconstruction is very difficult because the penis of the lectotype is bent and probably twisted also. Thus there is not a true sagittal section

of this organ. The major differences are as follows. I find the penis to be larger than drawn by Marcus, and the opening of the ejaculatory duct is more dorsal than terminal. Concerning the female system, Marcus shows the bursal stalk muscles to be divided clearly by the oviducts and shell glands into two distinct zones. I find this not to be the case. The muscles are continuous, although of varying thickness, and there are folds or creases in the muscle sheath which were caused, no doubt, by the contraction of the animal when killed. I do agree, however, that the muscle sheath is re-inforced ectally to the oviducts by an outer layer of longitudinal muscles, as in other species of the genus.

Neppia tinga is unique within the genus for its ventrally located testes. In general the testicular follicles are much smaller than those of the other species, even though they contain ripe sperm. The largest follicles, few in number, are between the gut diverticula and may reach almost to the dorsal side. Migration of the testes during maturation is known from some *Dugesia* species (see Ball, 1971), and the possibility that this may happen in *N. tinga* should not be discounted.

***Neppia wimbimba* (Marcus, 1970)**

Cura wimbimba Marcus, 1970: 12.

Dugesia (*Neppia*) *wimbimba* – Ball, 1974a: 377.

Type Material

Zoological Museum, University of Lund, Sweden. One specimen.

Distribution

Cape Province, South Africa.

Material Examined

None. Known only from the original description.

Remarks

Neppia wimbimba is unusual for its asymmetric oviducal openings into the bursal stalk and in the pronounced ental reduction of the strong musculature of the bursal stalk. In this last character the species is similar to *N. montana*.

Discussion of the Genus *Neppia*

In my earlier revision of the Dugesiidae (Ball, 1974a) the type species of *Neppia* was not designated unequivocally. It was my intention that for all the subgenera described therein the first-named species was to be considered as the type, and consequently *N. montana* is the type species of *Neppia*. Furthermore, I suggested tentatively (loc. cit.) that *Dugesia boehmigi* (Weiss, 1910) belonged in this genus. I have now had the opportunity to examine the types of this species, and I am of the opinion that it cannot be

so classified. The affinities of this species, and of the closely related *Dugesia hoernesii* (Weiss, 1910) will be considered in a separate publication.

The penial complexity, characteristics of the testes, and anatomy and histology of the copulatory apparatus suggest that this genus represents a monophyletic assemblage. Nonetheless *N. montana* and *N. schubarti* together show some differences from the remaining species of the genus. In both these forms the head is of high triangular shape with distinct pointed auricles, though these latter are not prominent in preserved specimens. Correlated with this is the fact that both *N. montana* and *N. schubarti* have long auricular sensory organs extending right across the auricles, and only at their posterior limits is there any evidence of epithelial folding. In the African species the head is of subtriangular shape, and the auricular sense organs form true pits (Marcus 1955). Furthermore, it is only in *N. montana* and *N. schubarti* that the testes extend to the copulatory apparatus; in all the other species the testes are entirely prepharyngeal. Similarly, the bursal stalk musculature is not as well developed as it is in some African species, notably in *N. tinga* and *N. paeta*.

That the closest relative of *N. montana*, from New Zealand, should prove to be a species from South America, *N. schubarti*, is of biogeographical importance in that it is consistent with the hypotheses of austral relationships which I have put forward elsewhere (Ball, 1974a). Another South American species, *N. falklandica*, seems more closely related to the African *Neppia* species in respect of external appearance and the male apparatus, but the anatomy and histology of the bursal apparatus are more similar to *N. montana* and *N. schubarti*. The atrial pockets or diverticula of such species as *N. schubarti*, *N. montana*, and to a lesser extent, *N. falklandica* (Westblad, 1952: fig. 24—C4), may have taxonomic significance in light of the fact that otherwise such pockets are known only from *Cura michaelsoni* and *C. patagonica*, two species in need of revision (p. 17).

Species Incertae Sedis

***Planaria ambigua* Böhmig, 1902**

Planaria ambigua Böhmig, 1902: 23.

? *Curtisia ambigua* – Marcus, 1946: 143.

Type Material

Unknown, possibly lost during the bombing of Graz.

Distribution

Punta Arenas, Chile.

Material Examined

None, known only from the original description.

Remarks

Marcus (1946) suggested that this could be a species of *Cura*, but it is quite impossible to be sure of this because the original description is so incomplete. The species is best regarded as a *taxon dubium*.

General Discussion

All the species discussed in this paper belong to the family Dugesiidae as defined by Ball (1974a). In my earlier study I conceded that this family was symplesiomorph, i.e., defined only by primitive characters, and I pointed out that the distinctions between the marine (Maricola) and freshwater planarians (Paludicola) were falling. Thus, on some southern hemisphere islands, marine planarians have been able to invade the freshwater environment in the absence of competition from indigenous freshwater forms, and new genera and species have evolved (Ball, in press). It is difficult to distinguish these from dugesiid forms by currently available definitions. The maricolan genus *Dinizia*, as represented by a new species described from the freshwaters of St. Helena, lacks a bursa copulatrix but has an anteriorly curved bursal stalk (Ball, in press). Strictly speaking, then, it is probursal and could well be allied with *Cura foremanii* (q.v.). The lack of pigment in the *Dinizia* species in question is not of phylogenetic significance. However, there is one fundamental difference between these Maricola and the Dugesiidae and this relates to the structure of the eye. In all Dugesiidae which possess eyes, each eye is composed of a pigment cup, comprising several cells, that embraces numerous retinal cells; there is no lens. An excellent description of this type of eye was given by Hesse (1897). In the Maricola, however, the pigment cup consists of one cell and contains only 1–4 retinal cells. The eye frequently is without a lens, but in some forms, including *Dinizia*, a distinct lens is present. Thus it is now possible to distinguish primitive Dugesiidae, such as *Cura*, from the Maricola, especially from those latter that have invaded freshwater. Moreover, the dugesiid eye represents an apomorph condition and thus the Dugesiidae are adequately defined.

Much of the classification of marine and freshwater planarians is based on the anatomy of the copulatory apparatus, and this may show wide variation. In the most primitive Maricola, and in the Dugesiidae, the terminal part of the bursal duct, which acts as a vagina, receives the discharge of the shell glands ectally to the openings of the oviducts. In both the Maricola and the Paludicola there has been an evolutionary tendency towards separation of the copulatory and glandular functions of this terminal part of the female genital duct. Hitherto we have known only one such tendency in the freshwater forms. It is possible to divide the freshwater triclads into two broad groups on the basis of the course of the oviducts and associated shell glands (Meixner, 1928). In the most primitive group (Meixner Types I, IIA, IIB), exemplified by the Dugesiidae, the oviducts and associated shell glands open into the female genital duct as described. In the most advanced group (Meixner Type III), exemplified by the Planariidae plus Dendrocoelidae, there is a common oviduct that receives the shell glands prior to opening into the roof of the male atrium quite independently of the vagina. It has been an important task to establish the phyletic link between these two groups.

Meixner (1928) felt that his Type IIC was the intermediate group. It comprised two Australian species, *Dugesia hoernesii* and *D. boehmigi* both described by Weiss (1910). The group was characterized by the fact that there was a common oviduct, receiving the shell glands, and opening into the posterior wall of the atrium at the base of the bursal stalk. In my detailed

discussion of this problem (Ball, 1974a) I declined to accept that Meixner's Type IIC was a natural group, and indicated that further work was needed urgently because, from the original descriptions, *D. hoernesii* and *D. boehmigi* did not seem to be particularly closely related. More recently, however, I have had the opportunity to examine the types of Weiss's species, and I find her descriptions to be in error on some points; corrective notes will be published elsewhere. I now agree that *D. boehmigi* and *D. hoernesii* are closely related and that a common oviduct opens into the atrium at the foot of, and posterior to, the bursal stalk. However, in both these species the shell glands open into the common oviduct and into the bursal stalk, as in *Neppia evelinae*, and so there has not been a true separation of glandular and copulatory function, nor is the vagina independent of the oviducal openings. Consequently, I do not accept Meixner's Type IIC as an intermediate group.

In *Romankenkius* gen. nov. there is another solution to this problem. There is a large diverticulum of the bursal stalk into which the shell glands open (Fig. 3A). Thus the copulatory part of the female duct is quite separate from the glandular part. This diverticulum is morphologically and histologically quite different from a common oviduct, and using criteria of position and structure I see no possibility of homology between the common oviducts of the Planariidae and Dendrocoelidae (sensu Ball, 1974a), and the glandular diverticulum of *Romankenkius*. The new genus cannot be interpreted as a link between the higher and lower freshwater triclads. The diverticulum may be compared with that of many *Procerodes* species (see Ball, in press), and some primitive limnic triclads such as *Rhodax* Marcus, 1946, and *Opisthobursa* Benazzi, 1972 (syn. *Dimarcus* Mitchell and Kawakatsu, 1972). In these more primitive genera, however, the musculature of the bursal stalk is not reversed.

The condition in *Romankenkius* thus is evolutionarily a new one, but the possibility that it is due to the re-expression of primitive and persistent genetic factors under new circumstances should not be overlooked. In this case, and using the terminology of Dougherty (1963), the characters would be metallogous. The fact that *Romankenkius* and some *Maricola* have adopted a similar solution to the evolutionary problem outlined in the above discussion is interesting, but it should not detract attention from the further fact that the *Maricola* as a whole exhibit many other solutions, particularly in the Uteriporidae and Bdellouridae, which are worthy of detailed analysis.

A detailed discussion of the evolutionary and biogeographical implications of the systematic revision presented here is made unnecessary by my previous analysis of southern hemisphere relationships within the paludicolous triclads (Ball, 1974a). My general conclusions that these triclads originated in the southern hemisphere, and that present-day distribution patterns most probably are a reflection of the disruption of Gondwanaland in the Mesozoic, still stand, although some additional remarks may be made.

Of the three genera discussed in the present paper, *Cura* undoubtedly is the most primitive by virtue of its bursal stalk musculature and simple penial anatomy (Ball, 1974a). Moreover, it is only within species of *Cura* such as *C. pinguis* and *C. foremanii* that we find the vitellaria extending far anterior to the ovaries. This condition is usual within the *Maricola*, but is rare in the

Paludicola (Meixner, 1928). Relationships within the genus are difficult to assess without access to specimens of *C. patagonica* and *C. michaelsoni*.

The patterns with the genera *Romankenkius* and *Neppia* are complex. They may be sister groups, but it is difficult to say which is plesiomorph and which apomorph. To derive a hypothetical common ancestor for both requires a minimum of two evolutionary steps from *Cura*: reversal of the bursal stalk musculature, and an increase in the size and number of the testes. Each requires a single step from this hypothetical ancestor. It is probable that intermediate forms remain to be discovered, and their nature and distribution would be of great interest. And it is for these reasons that the somewhat equivocal descriptions of *C. michaelsoni* and *C. patagonica* urgently need clarification from studies of new material.

Within the genus *Neppia* we find clearcut austral connections between New Zealand and South America on the one hand (*N. montana* and *N. schubarti*) and between South America and South Africa on the other (*N. falklandica* and *N. jeanneli*, *N. tinga*, *N. paeta*, *N. wimbimba*). The occurrence of *Neppia* in South America and in South Africa represents the first true faunal connection between these continents exemplified by freshwater triclads (cf. Ball 1974a). Nevertheless, this cannot be taken as evidence in support of Kawakatsu's (1968) view that the genus *Cura* sensu lato arose on the African continent from which it migrated transoceanically, because as pointed out previously (Ball, op. cit.), Kawakatsu's presumed paths of dispersal run contrary to the phylogenetic evidence at the generic level.

McDowall's (1973) criticism of my views on the biogeography of *Dugesia* s.l. and *Cura* s.l., as presented in a preliminary publication (Ball and Fernando, 1969), is unfortunate because he criticizes a position not taken. At no time have I concluded that the southern hemisphere distribution of *Dugesia* s.l. or *Cura* s.l. was a product of the former existence of Gondwanaland. It is my considered opinion only that the distribution patterns in relation to hypothesized phylogenetic relationships are consistent with the Continental Drift Hypothesis, and are *best* explained with its aid rather than by hypotheses of casual overseas dispersal. For example, the occurrence of *Dugesia* on the Crozet Islands, said to be of recent volcanic origin, does not prove that freshwater triclads disperse across seas (cf. McDowall, 1973: 88). Although it may be consistent with such a viewpoint, the great weight of evidence is to the contrary (Ball, 1974a). It is naive to believe that there should be a direct relationship between the geological age of isolated refugia, whether continental or oceanic, and the age of the occupying fauna. This point has been made so often, by Croizat (1962) for example, that it should not be necessary to repeat it.

It is quite possible that, with changing land and sea levels, the recent volcanic tip of Crozet represents but the most recent refuge of freshwater triclads, and perhaps other organisms (e.g., de Beauchamp, 1940b, Jeannel, 1961). In fact very little is known of the geology of the Crozet Islands. The available evidence suggests that they are geologically quite different from the Kerguelen Islands, from which freshwater triclads have not been reported, and that the Crozet Islands do not represent a younger stage in the history of oceanic volcanic islands (Bellair, 1964). These islands arise from great oceanic depths, an enormous mass of lava flows in the ocean floor, and

there is a deep submarine plateau along the western islands. Furthermore, from the above, and from the additional observation that the Prince Edward-Crozet Ridge is an extension of the South Madagascar Ridge, it is reasonable to postulate that the Crozet Islands are a continental fragment. As pointed out by Bellair (1964), however, it is by study of the ocean floor that progress will be made. The implication that biogeographers should rationalize their data so as to confirm with current geological opinion (McDowall, 1973: 91-92) is a viewpoint with which I disagree, especially as geologists themselves are by no means in agreement with each other. It is the triumph of Croizat (1958, 1962), a biogeographer much misunderstood by most recent workers, that he has stressed the independence and validity of biogeographical data.

The complexity of the austral connections exhibited particularly by the genera *Neppia* and *Romankenkius* is by no means unusual in the light of experience derived from other groups (e.g., Besch, 1964; Keast, 1971; Cracraft, 1973). New Zealand, however, does not seem to possess the degree of isolation suggested by some other studies (e.g., Keast, 1971). At the specific level *Cura pinguis* is widely distributed throughout Australasia. At the generic level *Neppia* is found in New Zealand as well as in South Africa and South America. Moreover, work in progress suggests that the genus *Spathula* Nurse, 1950, described originally and only from New Zealand, is a valid genus and may be represented by several species in southeastern Australia.

It is clear that the austral relationships of freshwater triclads are exceedingly complex and difficult to unravel. More sophisticated classificatory and biogeographical hypotheses than those already available can be expected only when we know much more concerning the planarian faunas of the Gondwanian continents, and the kind of taxonomic work needed is that which will lead to real knowledge of the species concerned and not merely to their diagnosis and naming.

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Summary

A new genus of freshwater planarian, *Romankenkius* gen. nov., is erected to contain two new species, *R. kenki* sp. nov. and *R. pedderensis* sp. nov., described from Tasmania. The genus is characterized by prepharyngeal testes and by the unusual relationships of the oviducts to the bursal stalk. *R. kenki* is unique within the Paludicola in possessing a free intrapenial prostatic vesicle comparable with that of many polyclads; *R. pedderensis* lacks such a vesicle. Both species possess a genito-intestinal communication.

A critical review of the related genera *Cura* Strand and *Neppia* Ball, including new distributional and morphological data, is provided, together with all available information on the location of the type material. In this review *Cura* is held to comprise the species *C. foremanii* (Girard), *C. pinguis* (Weiss), *C. azteca* Benazzi and Giannini, *C. michaelsoni* (Böhmig) and *C. patagonica* (Borelli). The last two species are assigned to the genus with some reservations. *Neppia* was originally proposed as a subgenus of *Dugesia* Girard to contain those African species formerly assigned to *Cura*, and one Australasian species. In the present review it is elevated to generic rank and enlarged. *Neppia* now comprises the species *N. montana* (Nurse), *N. jeanneli* (de Beauchamp) comb. nov., *N. falklandica* (Westblad) comb. nov., *N. schubarti* (Marcus) comb. nov., *N. paeta* (Marcus), *N. tinga* (Marcus), *N. evelinae* (Marcus) comb. nov., and *N. wimbimba* (Marcus). The realization that *Curtisia falklandica* and *C. schubarti* belong in *Neppia* reveals the first true faunal connection between South America and South Africa exhibited by the Paludicola.

Revised descriptions of some species are given and lectotypes are designated for *Cura pinguis*, *N. falklandica*, *N. paeta*, *N. tinga* and *N. evelinae*.

The systematic and biogeographical implications of the new data and opinions are discussed. It is concluded that the austral relationships of the Paludicola are more complex than previously recognized, although the distribution patterns exhibited remain consistent with, though not proof for, the hypothesis of continental drift.

Sommaire

Le genre *Romankenkius* g. nov. est instauré pour deux nouvelles espèces de Planaires d'eau douce provenant de Tasmanie: *R. kenki* sp. nov. et *R. pedderensis* sp. nov. Ce genre est caractérisé par la présence de testicules pré-pharyngiens et par l'abouchement, de type inhabituel, des oviductes et du canal de la bourse. Fait unique chez les Triclades paludicoles, *R. kenki* possède une vésicule prostatique, libre et intra-pénienne, assimilable à celle qui existe chez de nombreux Polyclades; celle-ci ne se retrouve pas dans l'espèce *R. pedderensis*. Une communication génito-intestinale s'observe en revanche chez les deux espèces décrites.

L'analyse critique des deux genres voisins *Cura* Strand et *Neppia* Ball est complétée par l'apport de nouvelles données concernant la distribution et la morphologie des diverses espèces pour lesquelles est également précisé le lieu de dépôt du matériel-type. Dans cette révision, au genre *Cura* sont attribuées les espèces *C. foremanii* (Girard), *C. pinguis* (Weiss), *C. azteca* Benazzi et Giannini, *C. michaelseni* (Böhmig) et *C. patagonica* (Borelli). Les deux dernières espèces sont rapportées à ce genre avec quelques réserves. A l'origine *Neppia* avait été proposé en tant que sous-genre de *Dugesia* pour inclure les espèces africaines préalablement considérées comme *Cura*, ainsi qu'une espèce d'Australasie. A présent, *Neppia* est élevé au rang de genre et renferme en outre les espèces *N. montana* (Nurse), *N. jeanneli* (de Beauchamp) comb. nov., *N. falklandica* (Westblad) comb. nov., *N. schubarti* (Marcus) comb. nov., *N. paeta* (Marcus), *N. tinga* (Marcus), *N. evelinae* (Marcus) comb. nov., and *N. wimbimba* (Marcus). Le fait que *Curtisia falklandica* et *C. schubarti* appartiennent au genre *Neppia* révèle, pour la première fois en ce qui concerne les Paludicoles, une véritable connexité de la faune d'Amérique du Sud et d'Afrique du Sud.

La description de quelques espèces est redonnée et les lectotypes sont désignés pour *Cura pinguis*, *N. falklandica*, *N. paeta*, *N. tinga* et *N. evelinae*.

La discussion porte essentiellement sur les implications systématiques et biogéographiques des nouvelles données. Il appert, pour conclure, que les affinités des Paludicoles australes sont plus complexes qu'elles ne l'avaient été reconnues jusqu'ici; cependant le schéma de distribution relevé vient confirmer encore, sans pour autant la prouver, la théorie de la dérive des continents.

Resumo

Um gênero novo de planárias d'água doce, *Romankenkius* gen. nov., e estabelecido para abranger duas espécies novas, *R. kenki* sp. nov. e *R. pedderensis* sp. nov., que são descritas da Tasmânia. O gênero caracteriza-se pelos testículos prefaringeanos e pelas ligações invulgares dos ovidutos com o duto bursal. *R. kenki* é único dentre os Paludicola pela vesícula prostática livre intra-penial, comparável à de muitos Polycladida; tal vesícula falta em *R. pedderensis*. Ambas as espécies tem comunicação genito-intestinal.

Revisão crítica dos gêneros vizinhos *Cura* Strand e *Neppia* Ball é dada, incluindo novos dados de distribuição e morfologia, mais todas as informações acessíveis sobre a localização do material típico. Nesta revisão *Cura* é tida como abrangendo as espécies *C. foremanii* (Girard), *C. pinguis* (Weiss), *C. azteca* Benazzi & Giannini, *C. michaelseni* (Böhmig) e *C. patagonica* (Borelli). As duas últimas são colocadas no gênero com certa reserva. *Neppia* foi originalmente proposta como subgênero de *Dugesia* Girard para abranger aquelas espécies africanas previamente colocadas em *Cura*, mais uma da Austrália e Nova Zelândia. Na revisão presente *Neppia* é elevada ao grau de gênero e alargada. Agora abrange as espécies *N. montana* (Nurse), *N. jeanneli* (de Beauchamp) comb. nov., *N. falklandica* (Westblad) comb. nov., *N. schubarti* (Marcus) comb. nov., *N. paeta* (Marcus), *N. tinga* (Marcus), *N. evelinae* (Marcus) comb. nov., e *N. wimbimba* (Marcus). O fato que *Curtisia falklandica* e *C. schubarti* pertencem a *Neppia* revela a primeira verdadeira ligação faunística entre a América do Sul e a África do Sul mostrada pelos Paludicola.

As descrições de algumas espécies são revistas e os lectotipos de *Cura pinguis*, *N. falklandica*, *N. paeta*, *N. tinga* e *N. evelinae* determinados.

A discussão trata especialmente das conclusões dos novos dados sistemáticos e biogeográficos. Chega-se a conclusão que as relações do hemisfério sul são mais complexos do que se julgava anteriormente; apesar—disto as distribuições continuam corroborando a hipótese da migração dos continentes, embora não são provas da mesma.

Zusammenfassung

Eine neue Gattung der Süßwasserplanarien, *Romankenkius* gen. nov. wird für zwei neue Arten, *R. kenki* sp. nov. und *R. pedderensis* sp. nov., aufgestellt, die von Tasmanien beschrieben werden. Die Gattung ist durch präpharyngeale Testes und durch die ungewöhnliche Verbindung der Ovidukte mit dem Bursastiel ausgezeichnet. *R. kenki* ist unter den Paludikolen einzigartig durch den Besitz einer freien, intrapenialen Prostatablase, die mit der vieler Polykladen vergleichbar ist. In *R. pedderensis* fehlt eine solche Blase. Beide Arten haben eine genito-intestinale Verbindung.

Eine kritische Übersicht der verwandten Gattungen *Cura* Strand und *Neppia* Ball wird gegeben, die neue Verbreitungs- und morphologische Daten enthält, zusammen mit allen verfügbaren Daten über die Aufbewahrung des Typenmaterials.

In dieser Übersicht soll *Cura* die Arten *C. foremanii* (Girard), *C. pinguis* (Weiss), *C. azteca* Benazzi & Giannini, *C. michaelsoni* (Böhmig) und *C. patagonica* (Borelli) enthalten. Die beiden letzten Arten werden mit einigem Vorbehalt zu dieser Gattung gestellt. *Neppia* war ursprünglich als Untergattung zu *Dugesia* Girard vorgeschlagen worden, um diejenigen afrikanischen Arten zu enthalten, die früher zu *Cura* gestellt worden waren, sowie eine australisch-neuseeländische Art. In der vorliegenden Übersicht wird *Neppia* zu Gattungsrang erhoben und erweitert. Jetzt enthält *Neppia* die Arten *N. montana* (Nurse), *N. jeanneli* (de Beauchamp) comb. nov., *N. schubarti* (Marcus) comb. nov., *N. paeta* (Marcus), *N. tinga* (Marcus), *N. evelinae* (Marcus) comb. nov., und *N. wimbimba* (Marcus). Die Feststellung, dass *Curtisia falklandica* und *C. schubarti* zu *Neppia* gehören, lässt die erste echte Faunenverbindung für die Paludikolen zwischen Südamerika und Südafrika erkennen.

Die Beschreibungen einiger Arten werden erweitert und Lektotypen für *Cura pinguis*, *N. falklandica*, *N. paeta*, *N. tinga* und *N. evelinae* bestimmt.

Die Diskussion betrifft hauptsächlich die systematischen und biogeographischen Folgerungen aus den neueren Daten. Es wird erschlossen, dass die südlichen Beziehungen der Paludikolen komplexer sind, als es bisher erkannt worden war, obgleich die gefundenen Verbreitungsbilder mit der Kontinentalverschiebungstheorie übereinstimmen, wenn sie auch keinen Beweis dafür darstellen.

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Key to Figures

bc	bursa copulatrix	nu	nucleus
bd	bursal stalk diverticulum	od	oviduct
bs	bursal stalk	oe	outer epithelium
cc	cushion cells	ov	ovary
cg	cement glands	pc	pigment cup
cm	circular muscle	pe	penis
cp	parenchymatic core of pharynx	ph	pharynx
de	dorsal epithelium	pi	pigment
dg	genito-intestinal duct	pv	prostatic vesicle
ed	ejaculatory duct	rc	retinal cell
fv	false seminal vesicle	rh	rhabdite
go	gonopore	sg	shell glands
id	intestinal diverticulum	ss	sensory slit
ie	inner epithelium	sv	seminal vesicle
lm	longitudinal muscle	sz	spermatozoa
ma	male atrium	te	testis
nc	ventral nerve cord	vd	vas deferens
ne	nerve tissue		

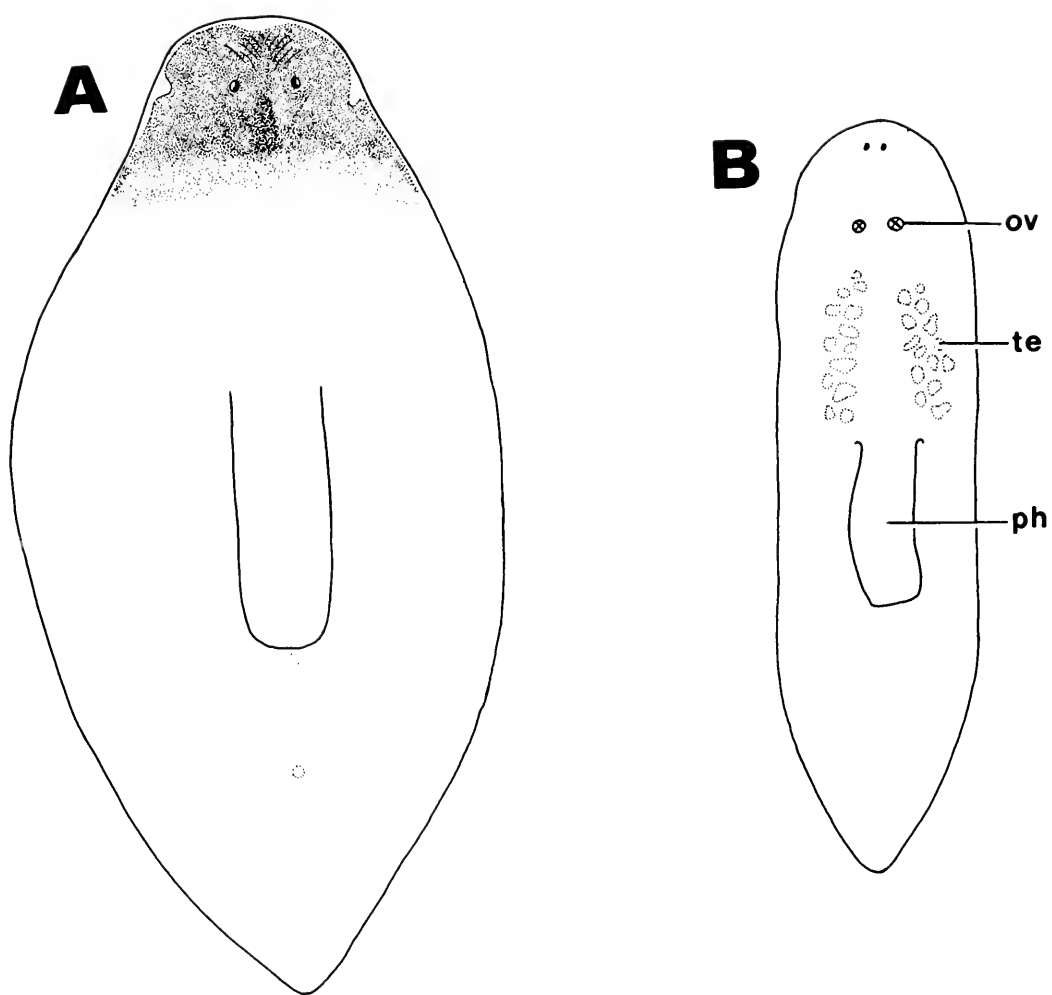


Fig. 1—The genus *Romankenkius*.

A. *R. kenki*, external features, length 13 mm.

B. *R. pedderensis*, showing shape and relative position of eyes, ovaries, and testes, length 8 mm.

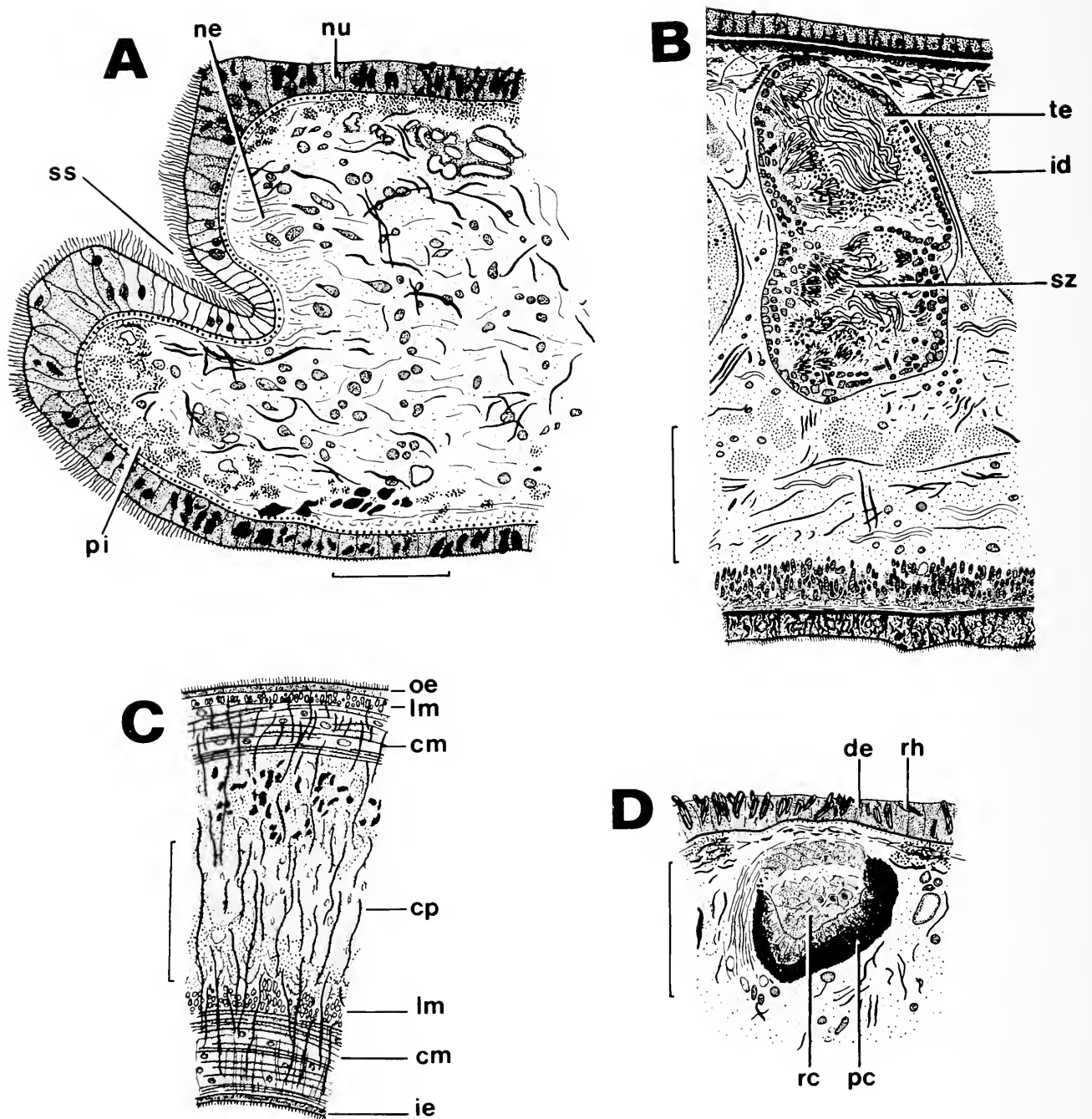


Fig. 2—The genus *Romankenkius*.

A-C. *R. kenki*.

A. Sagittal section through the anterior sensory slit of the holotype, scale 50 μm .

B. Transverse section through a testis, scale 100 μm .

C. Transverse section through part of the pharyngeal wall, scale 100 μm .

D. *R. pedderensis*, sagittal section through the eye, scale 100 μm .

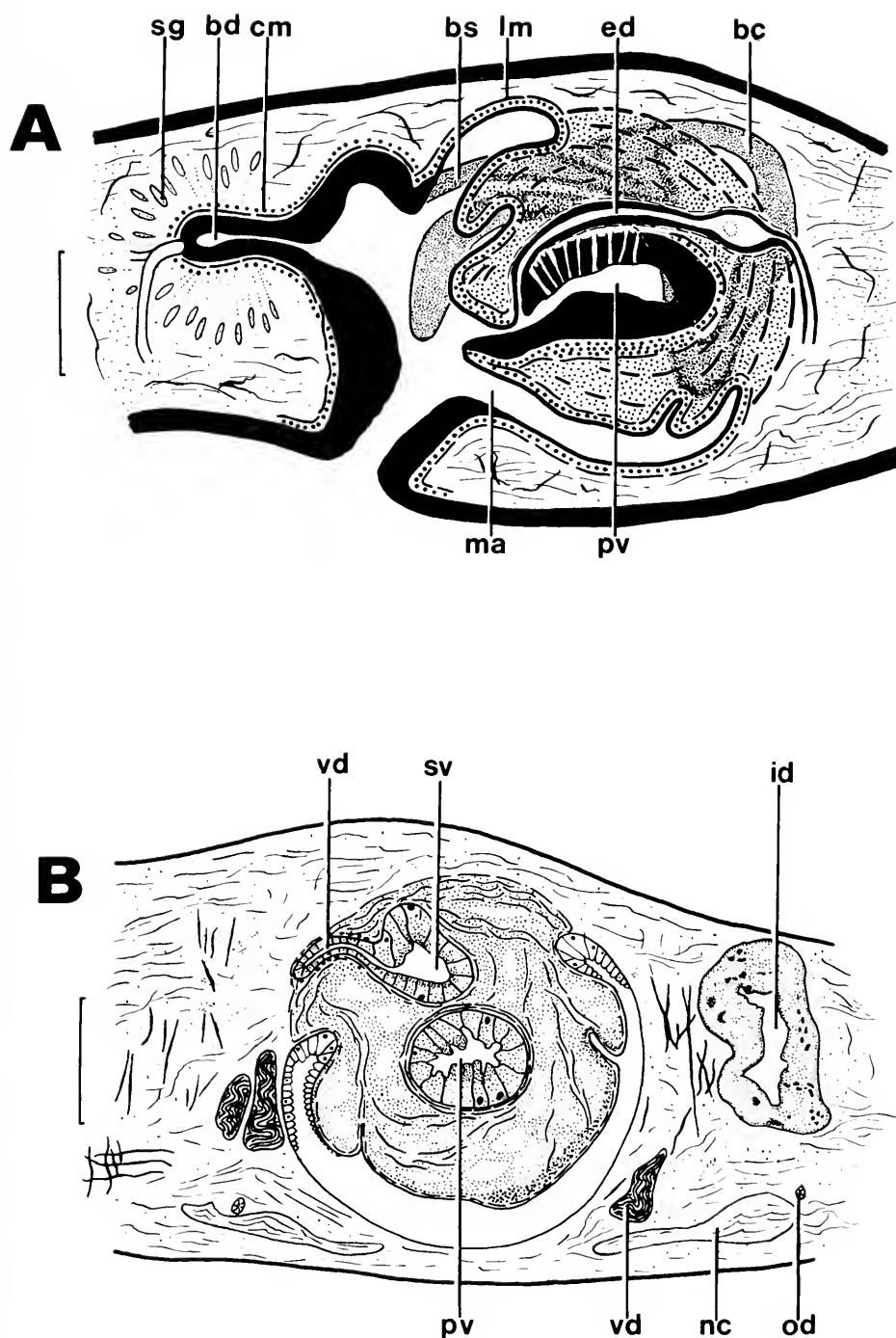


Fig. 3—The genus *Romankenkius*.

A-B. *R. kenki*.

A. Sagittal section of the copulatory apparatus of the holotype, viewed from the right side, scale 200 μ m. This drawing is reversed from the original slide for clarity, but the left-right parity has been maintained.

B. Transverse section through the penis, showing the entry of the left vas deferens, scale 200 μ m.

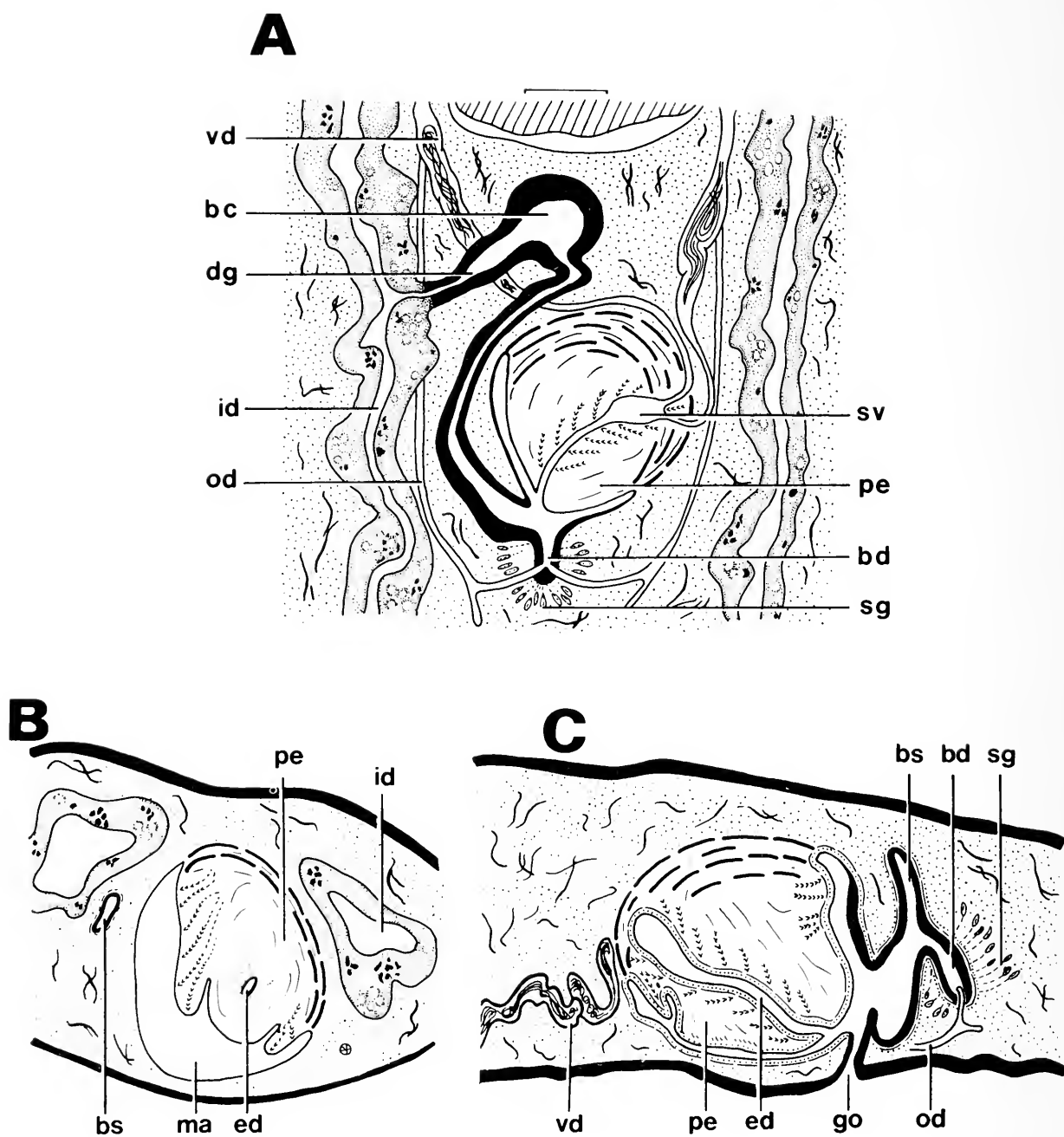


Fig. 4—The genus *Romankenkius*.

A-C. *R. pedderensis*.

A. Horizontal section through the copulatory apparatus, viewed from the dorsal aspect, scale 100 μ m.

B. Transverse section through the penis, scale 100 μ m.

C. Sagittal section of the copulatory organs of the holotype, viewed from the left side, scale 100 μ m.

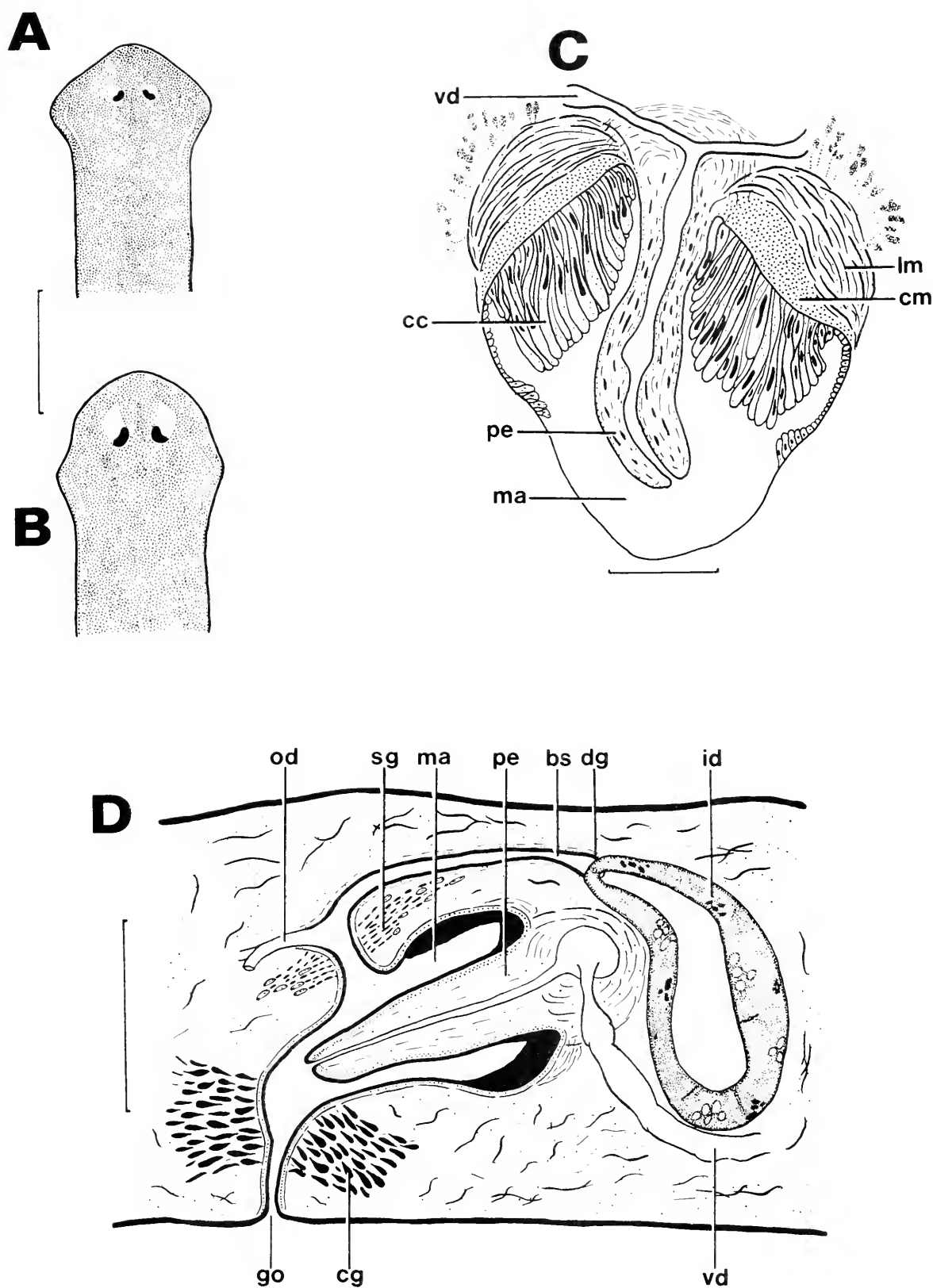


Fig. 5—The genus *Cura*.

A-C. *Cura pinguis*.

A-B. Specimens from Kentucky Creek, Uralla, N.S.W., showing variation in head shape, scale 1 mm.

C. Horizontal section, viewed from the dorsal aspect, through the penis of a specimen from Taumarunui, New Zealand, scale 50 μ m.

D. *C. foremanii*, sagittal section of the copulatory apparatus viewed from the right side, specimen from Newfoundland, scale 200 μ m.

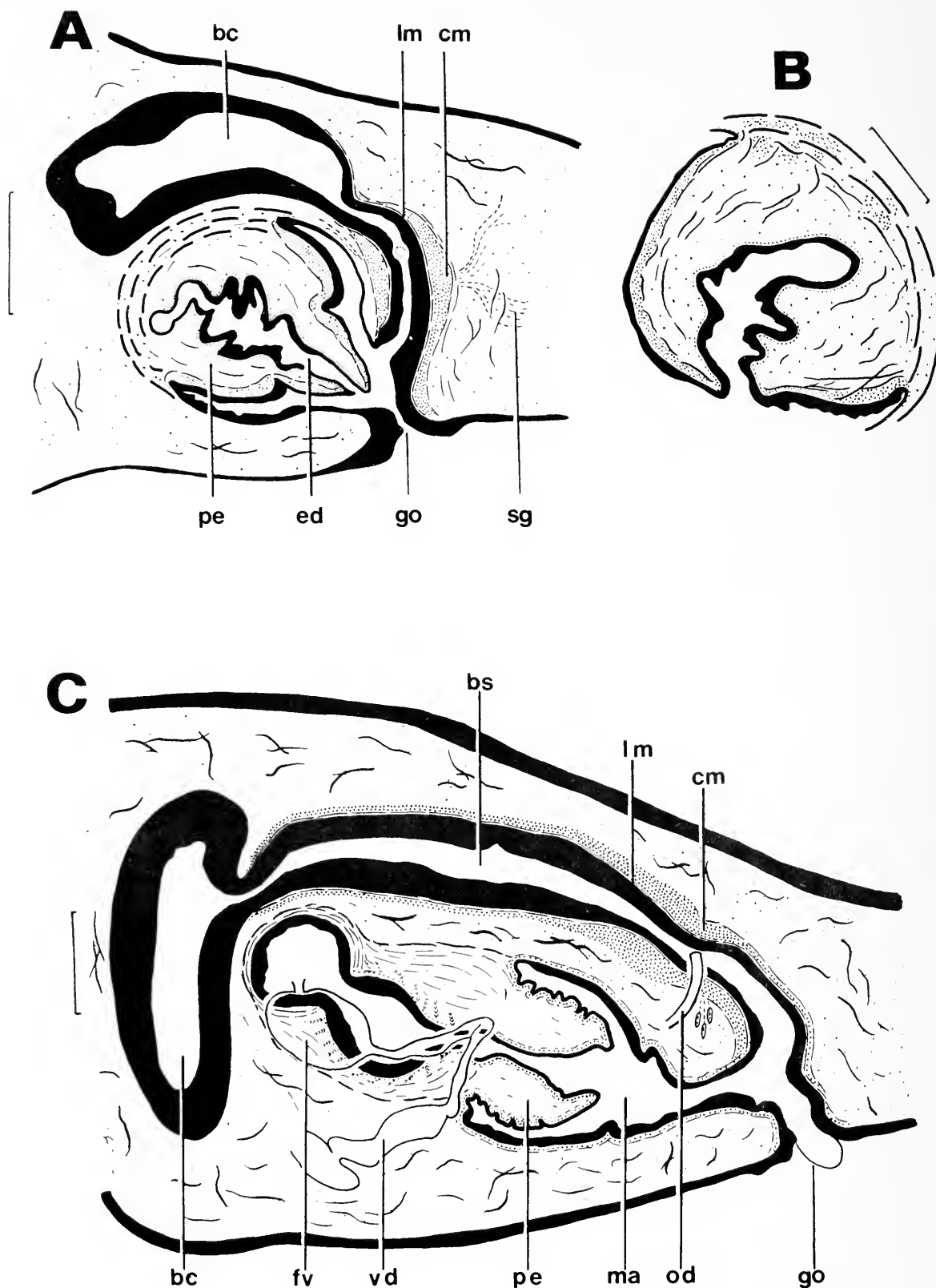


Fig. 6—The genus *Neppia*.

A-B. *N. jeanneli*.

A. Sagittal section of the copulatory apparatus, viewed from the left sight, of a syntype, scale 100 μ m.

B. Sagittal section of the penis of a second syntype, scale 100 μ m.

C. *N. falklandica*, sagittal section of the copulatory apparatus, viewed from the left side, of the lectotype, scale 100 μ m.

